

Transactions of the Royal Society of South Australia Incorporated

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TRANSACTIONS OF THE

**ROYAL SOCIETY
OF SOUTH AUSTRALIA**

INCORPORATED

VOL. 118, PART 1

Proceedings of a symposium entitled
**“CLIMATE CHANGE AND ITS IMPLICATIONS FOR
SOUTH AUSTRALIA”**
held on 11 November, 1993.

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CLIMATE CHANGE AND ITS IMPLICATIONS FOR SOUTH AUSTRALIA – INTRODUCTORY REMARKS

*BY W. D. WILLIAMS**

Summary

It is my privilege, as President of the Royal Society of South Australia, to introduce this important symposium on climate change and its implications for South Australia. In doing so, I wish first to welcome all participants and I extend a particular welcome to Sir Mark Oliphant, an Honorary Fellow of our Society. Our patron, Her Excellency the Governor, Dame Roma Mitchell, has indicated that Vice-Regal commitments preclude her attendance. I trust that all participants, students, distinguished scientists, or mere mortals like me, will find the symposium interesting, useful and a constructive addition to local debate on this most important matter.

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The Royal Society of South Australia held its first meeting in November 1880, shortly after Queen Victoria assented to the use of the word Royal. The Society, however, succeeded the Adelaide Philosophical Society formed much earlier, and indeed not long after the foundation of the State of South Australia. It was formed in 1853. Since those early years, the Society has met regularly, published scientific papers, maintained an extensive library, awarded grants for research or awards for meritorious contributions to science, and its Fellows have included most of South Australia's best known scientists.

The overall objective of the Society is the promotion and diffusion of scientific knowledge, and it is in support of this objective that the present symposium has been sponsored. I need hardly remind this audience that any change to the climate of South Australia will have profound, significant, and comprehensive effects on the South Australian environment, economy, social structure and public health — to name but the most obvious features that could be affected. It is to bring this to the attention of the community in general and its decision makers in particular that the present symposium is being held. Such an aim falls squarely within the overall objective of the Society. To promote further the views expressed, the papers presented are being published in this part of the *Transactions of the Royal Society of South Australia* and are also available separately as a book.

Of course, the symposium is only one of many that have been and are planned to be held to discuss climate change. At the international level, numerous meetings have been held, several scientific journals specifically target research on climate change, and there is an

international committee which reports regularly (IPCC: Intergovernmental Panel on Climate Change). Likewise, at the national level, considerable activity prevails. Indeed, the Australian Academy of Science is currently sponsoring a meeting in Canberra on the subject of climate change. The National Greenhouse Response Strategy was finalised in 1992, and at the State level, various government agencies maintain at least a watching brief on the subject; a number of natural and medical scientists, economists and others are actively interested in the subject, there is a Climate Change Committee (serviced by the Department of Environment and Natural Resources and including representatives from a wide variety of government departments) which reports regularly to Cabinet and has published several important documents (e.g. South Australian Climate Change Committee 1990, 1991) and, just a few years ago (1988), a wide ranging conference was held in Adelaide on the subject of climate change: I refer to *Greenhouse '88: Planning for Climate Change, Adelaide Conference* (Dendy 1989). Finally, I note the publication in November 1993 of *South Australian Greenhouse News*, Vol. 1, No. 1, the first of what is intended to be a regular series of newsletters with particular emphasis on South Australia. It is published by the South Australian Department of Environment and Natural Resources with the support of the Office of Energy.

Against this flurry of recent and ongoing activity one might ask, why should the Royal Society sponsor yet one more meeting to address the subject? What possible good can arise from another "talkfest"?

The answer is simple. First, research and views on this subject proceeds apace and there is a constant need to provide an opportunity for such research to be regularly aired for the benefit of the wider community. It is indeed half a decade since the last major meeting took place in Adelaide to discuss this matter.

Second, the Royal Society is quite independent of government departments, research institutions and universities, and is therefore in a unique position — indeed, has a special responsibility — to provide an opportunity for views to be aired which may not necessarily conform to the party line, current ideology or generally accepted scientific views. As will become obvious in some of the papers to be given, there are views held by some which do not agree with widespread views. [Sir Mark Oliphant, in a comment at the conclusion of the Symposium pointed to a recent article in *Nature, Lond.*, which pointed to the lack of any evidence of change in the present climate.]

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It is important for me to add that the views of speakers are not necessarily those of the Royal Society of South Australia or the institution to which the speaker belongs.

And a third reason behind this symposium is the constant need for the South Australian community, and through it, government departments and politicians, to be reminded of the need to *plan ahead* for possible change, which may, in any event, be more rapid than predicted. A recent article in the *New Scientist* (Nielsen 1993) documents some early results of the analysis of an ice core from Greenland which records detailed changes in the earth's climate over the past 250,000 years. According to scientists who investigated the core, present models used in predicting climate change may be too simplistic. In general, such models predict *gradual* change. Analyses of the core, however, suggest that a climate just a few degrees warmer than now may change very suddenly to become either significantly colder or warmer. In other words, we may be forcing

the present climate into an unsteady state when large natural changes in climate could be triggered by relatively small events. Whether such climatic instability has already started is a moot point. Bear in mind, however, that severe storms have cost insurance companies over \$60 billion over the past six years (Leggett 1993). Meteorologists have already begun to point to the increasing likelihood of an increased frequency of natural disasters following climate change in the next century (Zillman 1993).

I hope I have indicated sufficiently the need for and the importance of this symposium. All that remains for me to do is to thank the speakers for presenting their papers and the work involved in preparation, to thank my various colleagues, in particular Dr Margaret Davies, for her background support for the symposium, and to wish you all a good afternoon, *bon appetit* for the evening meal, and, since this is the last meeting of the Society for 1993, a Merry Christmas and Happy New Year.

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A BRIEF OVERVIEW OF CLIMATE RESEARCH

*BY PETER SCHWERTDFEGER**

Summary

Schwerdtfeger, P. (1994) A brief overview of climate research. Trans. R. Soc. S. Aust. 118(1), 3-7, 31 May, 1994.

The problems facing those attempting to generate reliable prognostic climate models is formidable. Good estimates of trends in concentration of all radiating atmospheric gases are necessary and these must be entered into a tested numerical model incorporating all of the important feedback processes. Included in these are the parallel processes occurring in the oceans. The simplest test of the prognostic prowess of a model is to run it backwards in time – a simple test of veracity that has not supported any modern long-term prediction model.

Key Words: climate change, models, radiating atmospheric gases, meteorology.

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Summary

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The problems facing those attempting to generate reliable prognostic climate models is formidable. Good estimates of trends in concentration of all radiating atmospheric gases are necessary and these must be entered into a tested numerical model incorporating all of the important feedback processes. Included in these are the parallel processes occurring in the oceans. The simplest test of the prognostic prowess of a model is to run it backwards in time — a simple test of veracity that has not supported any modern long-term climate prediction model.

KEY WORDS: climate change, models, radiating atmospheric gases, meteorology.

Introduction

Over a third of a century ago, I found myself as a freezing, fledgling geo-scientist, apprehensively prodding the frozen crust of Arctic sea ice below, in order to render advice on our mutual safety to my Red Indian companion, who gingerly guided the hungry dogs that, from meal to meal, dragged the sled which held our food and my bare-bones scientific equipment. We knew that we were venturing close to the brink of chaos when the supporting ice became less than six inches thick. My yelling out "150 mm" would only have generated dangerous confusion. The meteorological parameter of greatest concern to me then was the profile of temperature from the surface downwards, and for the following ten years, I remained interested in ice-bound temperatures in the Antarctic as well, and pondered on how these arose. At the time, these were generally regarded as activities unbecoming of atmospheric scientists, but with the growing relevance attached to the new science of *climate*, the perceived significance of the extent of polar ice, and its thermal as well as physical content has been dramatically changed.

During the last 25 years, I started to raise my head and examine the way in which the radiant energy incident on the Earth's surface was transferred not only to depths below but also to the atmosphere above. In the 1960s, many "real" meteorologists referred indulgently to the "boundary layer boys" (a phrase that the well known Princeton University theoretical meteorologist Joseph Smagorinsky used in a talk in Melbourne, when he unveiled the then excitingly new results of numerical modelling with enormous computers, leading to the promise of operational long-range weather forecasts). Smagorinsky was not sneering, he well knew that the most definitive transformation of energy from the Sun into other

radiative, conducted, convective, and evaporative forms takes place at the Earth's surface. Apart from the conducted heat which involves the material below the surface only, the three remaining fluxes drive that all important distribution zone, the diurnal boundary layer, the thickness of which can vary from millimetres to kilometres, depending on the season and time of day. Without the critical knowledge of the flows of energy into this boundary layer, resolved for a sufficiently finely spaced grid covering the area being modelled, every numerical meteorologist would be marooned. Therefore for some time, I continued to feel happy with the relevance of my work, delving in the lowest 10m of atmosphere blanketing the surface of the Earth.

Only ten years ago, as a result of my colleague Jörg Hacker bringing his combined knowledge of flying and meteorology to the Flinders University atmospheric research group, I became persuaded that there was more to meteorology than could be achieved by climbing with instruments to the top of a ladder. The experience of flying offers meteorologists definitive perspectives of the atmosphere, especially when the possibility of both making and viewing the results of actual physical measurements in real time allows important physical connections to be grasped. More than ever now, my heart bleeds for those meteorologists who spend all of their windowless lives hypnotically hunched in front of their computer screens.

The science of the *weather* was, in earlier years, often conveniently divided into *meteorology*, which involves statements about atmospheric conditions at various given times, including the future, when concepts of *forecasting* are involved, and *climatology*, which is concerned with quintessential summaries of meteorological conditions over specified places and periods. Applied sciences are strongly driven by public perceptions and wishes, in which matters, of course, scientists are increasingly not averse, if not forced, to offer their guiding influence. The last decade has seen the more geographical science of *climatology* fall into relative disfavour as the persuasive value of the study

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of climate, in being linked with the drama of inexorable trends and mystery of extremely long-term forecasts, has been heralded as an essential focus of serious attention.

Newspapers and television have popularised the subject of meteorology through the regular presentation of weather forecasts, and satellite images of the Earth have helped greatly in generating an appreciation of the global nature of meteorological processes reflected in visible cloud structures. There is no doubt that an advance knowledge of details of meteorological conditions is important in many areas of human endeavour. Over relatively short terms and for specific areas such as landing grounds, aviation safety depends on it. Forecasting also influences many other commercial operations, including those connected with agriculture, the manufacture of icecream and drinks, the selection of routes for shipping as well as personal choices regarding clothing and recreational activities. As a result, the concepts of *meteorology* and *forecasting* have become almost synonymous in the public mind.

However, more general climatological summaries also help to guide the public, particularly travellers, even though a little caution is required when too little detail is offered. For example, the bald statement that Adelaide's mean January temperature is 23°C could easily prove deceptive to a naïve visitor, when it is known that the mean maximum temperature is 30°C and the mean minimum 16°C, with extreme values of these two parameters of almost 48°C and 7°C having been recorded. Equipped with this additional information, the intending traveller might obtain some idea as to what types of clothing to pack. An even more useless piece of "stand-alone" climatological information, except perhaps to wine-makers needing to be assured that the temperatures maintained in deep cellars are beneficial to the maturation of their products, is that Adelaide's mean annual temperature is 17°C. Responsible and useful climatological compilations usually aim to provide envelopes for ranges of values within which parameters of interest might be expected to lie. The choice of these parameters as well as the time scale will depend on the purpose of the application. For example, for agricultural decisions, information about *rainfall*, *temperature*, *solar radiation* and *windiness* (including likely extremes) is important. In the light of the present knowledge of the Earth's regional climates, it is easy to overlook the achievement of colonial planners such as Colonel William Light, the founder of Adelaide, who within six weeks of arrival, barely in advance of the first European settlers, was able to assure himself as to the general nature of Adelaide's climate and to realise that it was the only location near the coast of what had been designated as South Australia where a city based on 19th century technology could be established.

The need for information on weather in general terms is readily accepted for seasonal forecasts for agricultural and water resources planning. Inevitably, because of the historically observed link between protracted extremes in meteorological conditions and the economy, the possibility of reliably ascertaining long-term trends is an attractive proposition. Therein lie the origins of the clamour for, and the justification of, modern climate research.

Meteorological processes occur on many different time-scales. The two most familiar of these are the variations in insolation which result in the annual cycle of seasons and the daily rising and setting of the sun. Both are associated with systematic insolation changes which result in every other meteorological parameter experiencing consequent variations. Changes on other time-scales are far less predictable. At the high frequency end, turbulence is best described by using statistical expressions. Low frequency meteorological changes have been discovered in geological studies of the history of the Earth with distinct climatic events being separated by from thousands to millions of years. On this scale, geologists and glaciologists have long led meteorologists with the intensity of their interest.

Systematic periodic meteorological changes can be summarised by the climatology of the periods under consideration. Prior to the development of modern methods of recording meteorological values, the descriptions of historians, including the authors of the *Old Testament* offer investigators of past climates a wealth of information. For example, during his years in Egypt, by warning of the seven years of famine to follow years of plenty, Joseph issued his Pharaoh with the first recorded successful long range weather forecast. The *Little Ice Age* of the Middle Ages is a well recorded historical fact, easily verifiable through studies of the advance and retreat of Alpine glaciers. Only in the 20th century have mine-shafts, last worked some 600 years ago, become visible again with the retreat of these glaciers which began in the 19th century. Modern visitors to the "Belvedere Hotel" which, a hundred years ago dramatically overlooked the Rhone Glacier in Switzerland, may well ponder on how long powerful binoculars will suffice to offer a glimpse of the glacier's snout following its dramatic recession. It was this same "Middle Ages" ice age which contributed substantially to the elimination of the Viking colonies from Greenland at about the same time that Christopher Columbus was busily diverting European attention to warmer parts of the New World. Bryson & Murray (1977) offer accounts of climate changes and the consequences thereof to various civilisations over several thousand years of documented history.

There is absolutely no doubt that the climate of the Earth is and has always been changing (Brooks 1949). However, what has also been changing during the last

two decades is the public perception of the nature of climate changes and concern that the contribution to these by human activities may greatly overshadow natural random trends. Quick to respond to such concerns, many atmospheric scientists have sought to quantify and offer physical explanations for both primary observations and assumed consequential changes. Changes of climatic parameters occurring "naturally" are on seemingly random time scales because of the different rates governing the physical "feedback" systems which link most, if not all, processes in the atmosphere. The vast range of these processes, and their interactions, offer the perfect recipe for chaos.

The subjection of past climatic data to frequency analysis in the hope of obtaining cyclically repetitive messages has been in vain. My Flinders University colleagues, John Bye, Roland Byrnes-Scott and Adrian Gordon have demonstrated this phenomenon of randomness in an unusually direct way. They have translated random levels of net-insolation, by means of a simple, physical computer model in which atmospheric and oceanic momentum are plausibly coupled, into time series of air and sea temperature which over a period of several simulated centuries display an uneasy superficial resemblance to actual observations.

Were the Earth to be a simple, heat conducting hollow shell; similar perhaps to early artificial satellites, but not even containing a suffering dog, then meteorology would be simple: the surface temperature would be the only reportable factor, and it could be calculated from a knowledge of the *solar constant* (which in fact is not quite constant) and the measurable radiative properties of the satellite surface. The result is commonly referred to as the *planetary temperature* and the two important planetary radiative properties in which this temperature is related are the *albedo* or surface reflectivity toward the wavelengths of solar radiation, which are predominantly visible and the planet's *emissivity*, a factor which determines the efficiency of the export of radiative energy, mainly in the infra-red range of wavelengths, out to space. Otherwise, this loss of radiant energy is determined only by the temperature, a fact discovered by Newton three centuries ago and quantified by Stefan and Boltzmann late last century. This relative meteorological simplicity is further enhanced by its instantaneity; a thin hollow planetary shell cannot store any heat energy and the coupling of temperature and radiational events occurs without any delay.

By virtue of its atmosphere, not to mention its solid, heat storing mass, our real Earth has made this simple business far more complicated. For example, the diurnal delay between maximum insolation at the local, geographical noon and the maximum air temperature, which may occur 2.5 hours later is almost entirely

ascribable to the thermal admittance or conductive-capacity of the ground. The Earth's surface itself does not have a uniform albedo; this varies from 3-4% over large parts of the ocean to 80-90% over freshly fallen snow. The level of heat storage depends on the heat capacity and thermal conductivity of the material beneath the Earth's surface, but these conductive processes cannot compete with the efficiency of both horizontal and vertical energy transfer mechanisms within the Earth's dynamic atmosphere. Viewed from space, the clouds which result from the presence of water vapour are the most dominating and reflective feature. Clouds are largely responsible for the Earth's average albedo being about 34%. As in the case of the hypothetical, hollow, atmosphereless planet discussed earlier, the 66% of the incident solar energy which is accepted by the Earth can also be used as the basis for the calculation of a steady state planetary temperature; in fact this turns out to be about -22°C. Although this figure has real meaning in terms of the Earth's temperature when observed from outer space, it is difficult, unless resting on a polar ice floe, to appreciate its significance back on Earth itself where the areally integrated mean surface temperature is about 15°C. The corresponding figure in upper atmospheric levels which still emit significant amounts of infra-red radiation is about -60°C. It is essential to realise that the planetary temperature must be regarded as a radiatively weighted mean over the entire thickness of the atmosphere.

The atmosphere, because it contains poly-atomic gases, which partially absorb and re-emit their characterising bands of infra-red radiation which the Earth's surface transforms from absorbed incident solar radiation, greatly modifies the simple, 2-dimensional picture of planetary temperature. Simpson (1927, 1928, 1929) was one of the first to quantify, in terms of spectrally selective absorption, the *Greenhouse Effect* which is essentially responsible for the mean temperature at the surface of the Earth being approximately 37°C warmer than the planetary temperature. The over-whelmingly important gas in this radiative process is water vapour, H_2O . Understanding how this process contributes to the distribution of temperature within the atmosphere is difficult enough in itself, because the concentration of this vital vapour varies with both location and time. Its concentration and temperature in turn determine the existence of clouds, which increase the reflection of incoming solar radiation, thereby generating the fundamentally important feedback process of the Earth's surface becoming shaded below, thereby reducing its temperature and consequently also the level of evaporation. All of these linked steps occur neither instantaneously nor at rates which can be uniquely specified. The physical clarity of the entire process, which is most readily comprehended in a single,

vertical dimension, becomes obscured by large scale horizontal advective processes, of which the winds near the ground and movement of clouds above are the most obvious manifestations. The variability of H_2O in our atmosphere results from the fact that it readily changes from vapour to liquid and even solid phases within the range of temperatures encountered on Earth, all forms having strikingly different mobilities.

There are other gases which contribute to the atmospheric *Greenhouse Effect*, which it should be emphasised, is significantly different from the market garden type, the latter having enclosing impermeable membranes to inhibit both convective and water vapour losses from the system. The additional gases are also poly-atomic, that is they have three or more atoms per molecule and are present in concentrations which are small compared to that of water vapour. In the absence of strongly localised sources of production and of sinks, which absorb them, these gases are considered to be uniformly mixed with the other, dominating gases of the atmosphere, such as oxygen and nitrogen. All of the early radiation models of the atmosphere in focussing on the importance of water vapour, designed to consider only carbon dioxide, CO_2 , as being of even secondary importance in their schemes. Other members of the atmospheric family of poly-atomic gases, including methane, oxides of nitrogen and ozone were regarded as negligible in influence. The importance accorded these gases changed dramatically following the first few years of observations, when these became available during the 1970s, from a global network of monitoring stations which detected steady increases in the mean annual concentrations of particularly CO_2 and CH_4 in the atmosphere. (e.g. M.I.T. 1971). These are readily explicable in terms of the ever increasing combustion of fossil fuels, the rotting and burning of the world's remorselessly felled remnant forests, and the flatulence of the world's burgeoning herds of tame ruminants. It is reasonable to accept that with significantly greater concentration levels, these gases should be included in the accounting of radiative energy transfer and heating. The success with which this can be done also depends on the ability to identify the nature and magnitude of all of the feedback processes.

With the acknowledged increase of the "lesser" radiatively important gases, arises the question as to the means whereby the atmosphere is also able to continuously shed part of the concentration. That this must always have been so is clear since CO_2 and CH_4 have both been released to the air at least since life began on Earth, even in times when their mean concentrations were relatively stable. On the basis of current estimates of the global rates of CO_2

production and knowledge of its actual concentration in the atmosphere, it is a simple matter to calculate the rate at which one of the Earth's feedback systems is dealing with the "fixing" of ever increasing loads of this gas by, for example producing carbonates as a result of the dissolving of the CO_2 in water. This has long been a fertile field of investigation for geologists. However, it is now apparent that this process is not coping with all of the CO_2 currently being produced, so that its atmospheric concentration is continuing to increase.

In summary, the problems facing those aiming to generate a reliable prognostic climate model are quite formidable. It is necessary to have good estimates of the trends in concentration of all radiating atmospheric gases and to ensure that these are entered into a tested numerical model which incorporates all of the important feedback processes made even more complex by the appreciation in recent years that models of global atmospheric circulation cannot function without consideration of the parallel processes occurring in the oceans. The simplest test of the prognostic prowess of a model is to run it backwards in time. When Uwe Radok and Dick Jenssen developed Australia's first numerical short-term weather forecasting model at Melbourne University in the late 1950s. (Jenssen 1962¹), they used this simple and honest procedure. To the best of my knowledge, no modern long-term climate prediction model has yet withstood this simple test of veracity.

In spite of the fact that one stroke of a U.S. presidential pen can have greater consequences for the Australian agricultural economy than even some of the more adverse predictions offered by the proponents of climate models currently in vogue, I believe that climate research is important. I also believe that some of the recommendations of those whose faith in current model predictions is close to absolute, in which a radical reduction in the global scale of combustion is urged, deserve substantial endorsement, particularly where this may lead to a deceleration of the senseless destruction of the world's forests. Others may applaud the development of more vegetarian habits by the increasingly carnivorous human race, whether or not a reduction in global cattle numbers has any ultimate significant impact on climate trends. I do, however, find it regrettable, that the stronger proponents of climate research have disproportionately triggered a wide range of political mechanisms by means of potentially alarming information, without proper substantiation, apparently to generate and maintain high levels of public attention. So far the main result appears to have been to generate public confusion between the concepts underlying the *Greenhouse Effect* and the *Ozone Hole*. I well recall two remarkably different lectures held within the space of a single decade in the very same University of Adelaide, by an

¹Jenssen, M. I. D. (1962). Ph.D. Thesis, Meteorology Department University of Melbourne Unpubl.

internationally acclaimed visiting atmospheric scientist. The first of these chillingly foretold of an impending *Ice Age*, the second unabashedly warned of *Greenhouse warming*. Of course all scientists need public attention in order to survive, but for credibility to be maintained, science normally needs to disclose verifiable results, even if these may require interpretation in a manner conducive to greater public appreciation. It is dangerous for any branch of scientists to test popular indulgence too far and in the case of atmospheric scientists, to allow the public to lose sight of the many other useful purposes their scientific endeavours both continue to and could be offering, particularly in non-long-term prognostic ventures. With public and

political attention rivetted on such matters as burping bulls in Brazil and the saturation of the ever expanding seven seas with soda water, it is easy to overlook the multiplicity of climate-related environmental problems closer to home, where appreciation of diverse themes, ranging from the security of vital water supply catchments and the impact of large-scale land management policies on regional climates (and vice versa), to detailed investigations of the actual physical and chemical processes constituting the links of the complex chain of events loosely described as climate, are vulnerable to chaotic diversionary forces which thrive in confused societies.

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MODELLING CLIMATIC CHANGE AND VARIABILITY

*BY ROBERT J. ALLAN**

Summary

Allan, R. J. (1994) Modelling climate change and variability. Trans. R. Soc. S. Aust. 118(1), 9-15, 31 May, 1994.

Recent interest in climatic change has engendered considerable debate about the enhanced greenhouse effect and its possible global impacts. Numerical computer models of the climate system are important tools in the scientific assessment of the enhanced greenhouse effect. This paper briefly reviews the model development and approaches used to simulate the nature of anthropogenic changes and natural variability in the climate system. Research in Australia is given particular emphasis.

Key Words: climate change, numerical computer models.

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Introduction

The global climate system involves closely linked interactions between the atmosphere, oceans, cryosphere and the biosphere. This system is driven by energy derived from solar radiation, with the net incoming energy being balanced by that which is lost to space. The nonlinear and highly dynamic climate system is a consequence of the redistribution of this energy by thermodynamics and the forces of motion derived from the planet's rotation. Any fluctuations or changes in the climate system can be brought about by external forcing, or by processes and readjustments intrinsic to such a closely coupled nonlinear system. Since the system is finely balanced, what might appear to be minor changes in any part of the system can cause large changes in its character.

Until the latter part of this century, attempts to understand the climate system, and the variations and changes in it, were pursued through observational studies and the development of physical theories of the interactions and motions governing it. With the advent of, and improvements in, computer technology, efforts to produce computer models of the climate system have expanded rapidly. Much initial modelling work focused on the need to improve day to day weather forecasts using models capable of resolving synoptic scale features in the atmosphere. However, the longer term envelope of weather events that constitutes the climate has now become a significant area in numerical modelling. Concerns about the enhanced greenhouse effect and a need to understand natural fluctuations in the climate system have seen a strong focus on the development of models able to capture the processes governing interactions inherent in the climate system. Such interactions are shown schematically in Fig. 1.

This paper provides an overview of the important characteristics of numerical models that have been used to improve the scientific understanding of changes and fluctuations in the climate system. It focuses on both

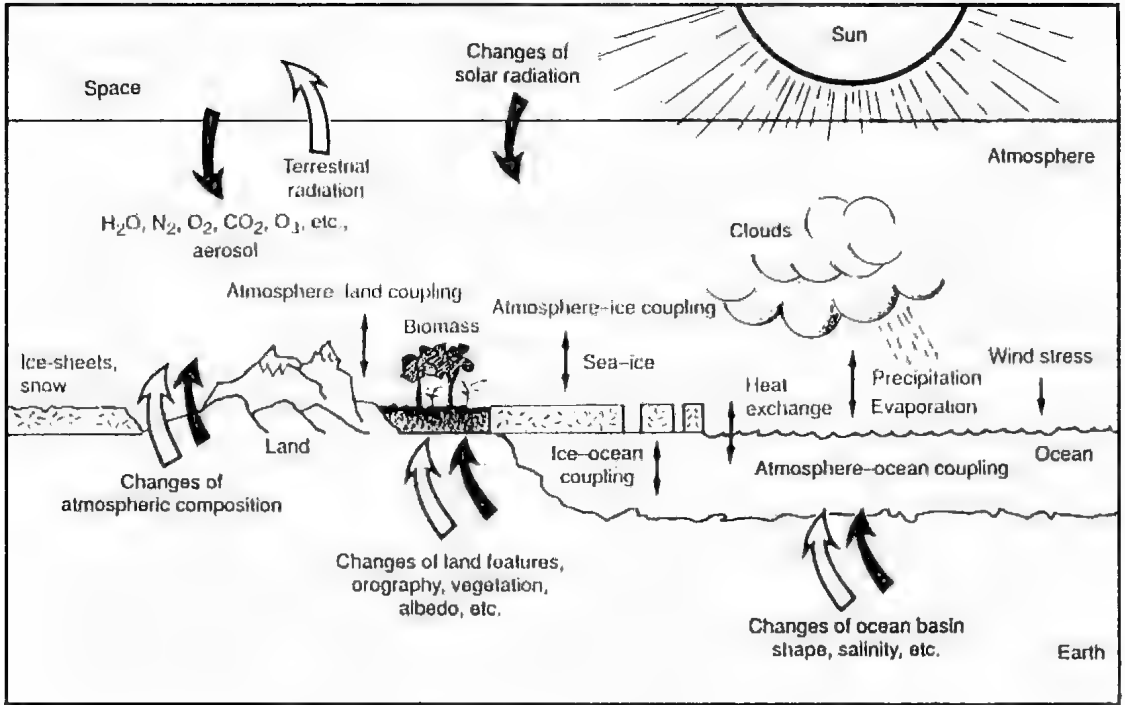
international efforts and the progress being made in Australia to examine potential climate problems using numerical computer models.

Low order models

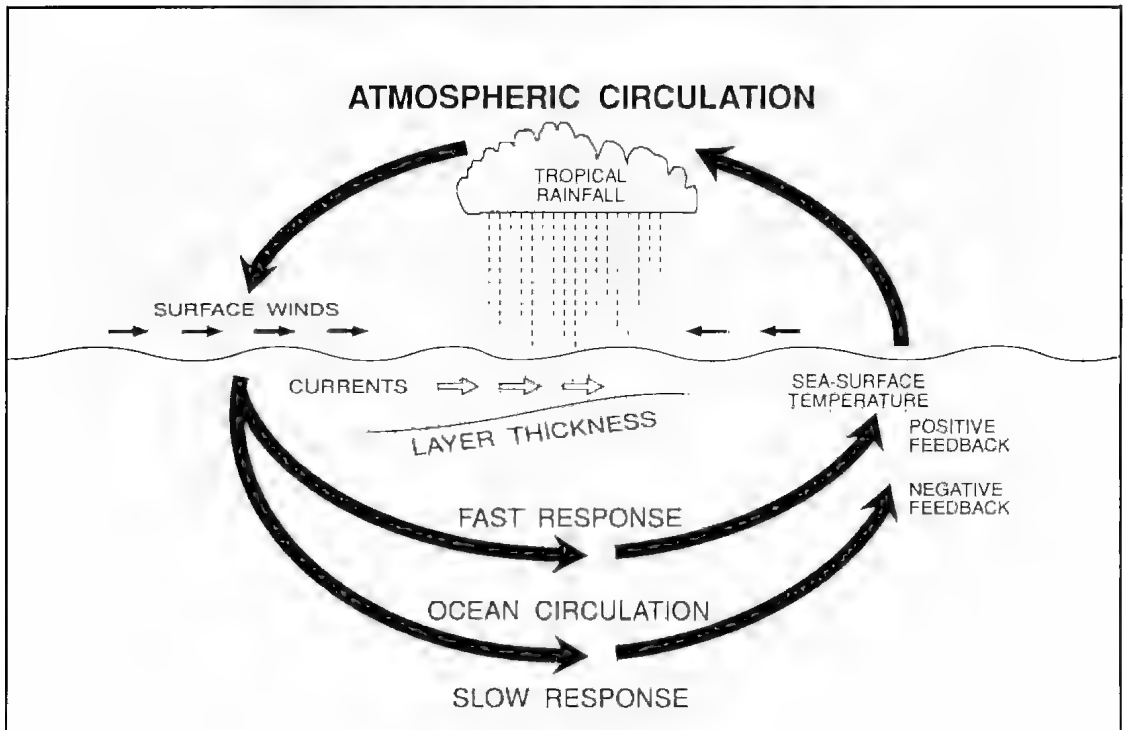
Some models have been developed to improve understanding of particular features that dominate the climate over regions of the globe and for various periods of time. Such models use what are often called "primitive" forms of the basic physical dynamics that are necessary to encompass the processes underlying climatic phenomena. These computer models contain sets of mathematical equations describing the most important physical interactions at each point on horizontal and vertical grids of points that cover the region in which the climatic feature occurs. All the equations governing the physical properties of the phenomenon are solved at time steps indicative of the observed nature of the processes being examined. In this way, a model of the real system is built up. However, such models are only as good as the mathematical resolution of the dynamics of the feature being modelled. Some real processes are relatively easier to describe mathematically and their interactions are known. Others are difficult to capture fully, or the present physical understanding of them may be limited. In general, low order models have focused on resolving the important atmospheric and/or oceanic character of a particular climatic phenomenon.

Perhaps the most concentrated emphasis in this area has been in the construction of low order models aimed at capturing the essence of El Niño-Southern Oscillation (ENSO) events. The ENSO phenomenon is a large-scale ocean-atmosphere interaction that occurs irregularly and is centred in the Indo-Pacific basin. It involves a close coupling of the important features of the climate system across this region and has significant impacts in the marine and terrestrial environments. Some of the main variables and feedbacks known to operate during ENSO events are shown schematically in Fig. 2, and a review of the phenomenon can be found in Allan (1991).

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COUPLED OCEAN-ATMOSPHERE



Most low order models of ENSO have focused on the Pacific Ocean region bounded by the subtropics in both hemispheres. Such models are very simple, with minimal physical representation of the atmosphere (often only two layers in the vertical) and a construction designed to resolve the basic dynamics of the ENSO phenomenon alone. The building of models in this context has required substantial resources and particular recourse to observational studies and dynamical theories which provide a conceptual framework of the physical processes likely to underlie the phenomenon. At present, there is no firm theory describing all aspects of ENSO events, but rather a dynamically consistent understanding of *some* of the important processes governing its behaviour. Current models of ENSO have been built under this constraint. More recent developments in low order coupled ocean-atmosphere models have seen improvements in the ability of these tools to predict ENSO behaviour. The most comprehensive review of the current status of ENSO modelling is given in Neelin *et al.* (1992). In Australia, such work is perhaps best characterised by the low order model developments at the Bureau of Meteorology Research Centre (BMRC) (Kleinman 1991, 1993). Further progress can be expected as the underlying dynamics powering ENSO episodes become better understood, and the capabilities of models to represent such complex processes develop further.

General Circulation Modelling

More detailed numerical models for climatic research are the General Circulation Models (GCMs), which are three dimensional models of the global climate system. These models represent interactions between features of the climate system through a series of mathematical equations on a spherical grid. The grid, representing a latitude by longitude array, is repeated in the vertical plane over the desired number of levels or layers through the depth of the atmosphere. This structure is shown in Fig. 3, and provides the framework within which the model simulates the dominant processes of the climate system over time. Physical processes and interactions are calculated at each grid point simultaneously in the active model. In addition, in some models important oceanic links to the GCM atmosphere are mimicked by including

a "slab ocean" in the model. This is a 50 m deep layer covering the Earth's oceans that performs like a well-mixed oceanic "near surface" layer. However, sea surface temperatures simulated by this approach must be continuously corrected to take account of the heat transport by horizontal currents and deep ocean processes. This is termed a Q-flux correction to the GCM. Using this technique and given the constraints mentioned, an evolving simulation of the Earth's climate is produced by the model that captures many observed aspects of the climate system. Detailed specifications of the CSIRO Division of Atmospheric Research (DAR) and the BMRC GCMs that have been developed in Australia, are given in McGregor *et al.* (1993b) and Hart *et al.* (1990).

Despite the relatively sophisticated nature of GCMs, they are coarse in their spatial resolution with gridpoints spaced at around 500 km apart and vertical levels representing the atmospheric structure usually limited to between 10-20 layers. As a result of these spatial restrictions imposed by limitations of computing resources, many smaller features of the climate system such as tropical cyclones and deep cyclonic systems cannot be resolved by GCMs. Another important problem that stems from the spatial limitations is that some physical processes, such as those relating to aspects of cloud physics, cannot be fully resolved and are parameterised in these models. These factors limit the current capabilities of GCMs to capture the full intricacies of global climate. At present, for example, GCMs are unable to produce realistic ENSO events. Nevertheless, it must be realised that these are early generation models and that many of the large-scale aspects of the real climate *are* seen in the current GCM simulations.

An important advance in the development of GCMs is the coupling of atmospheric and oceanic models (formulated similarly to the GCMs) in order to capture more of the essential elements responsible for observed climatic patterns. Currently, such coupled models require correction for fluxes of energy, momentum and moisture exchange between the atmosphere and the oceans if they are to resolve full ocean-atmosphere interactions. Most simulations of enhanced greenhouse effect conditions with current coupled ocean-atmosphere GCMs have used flux correction. However, as noted in the section on low order models, coupled models provide the basis for a more realistic

Fig. 1. TOP. A simple schematic view of the major interactions in the global climate system.

Fig. 2. BOTTOM. A schematic diagram of ENSO interactions involving major oceanic and atmospheric variables in the Pacific Basin. The two responses (fast and slow) in the ocean refer to different feedbacks resulting from the nature of the dynamical waves generated by tropical ocean-atmosphere interactions inherent in the phenomenon.

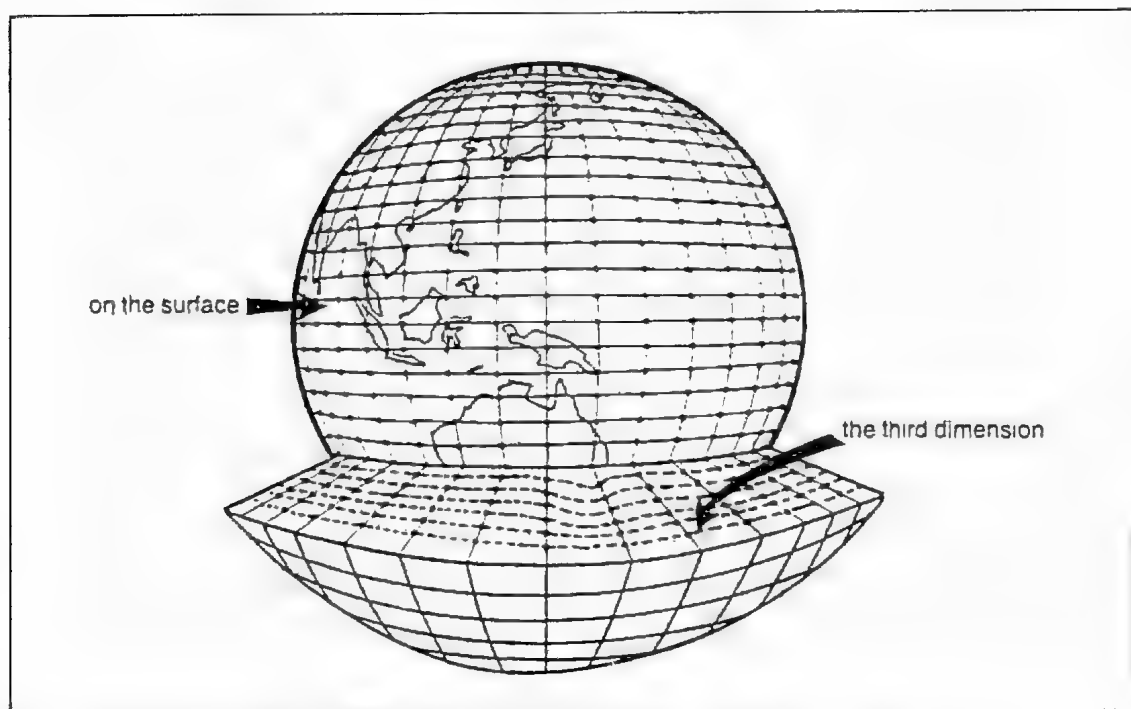


Fig. 3. A schematic representation of a GCM as it divides the earth into a regular three-dimensional grid.

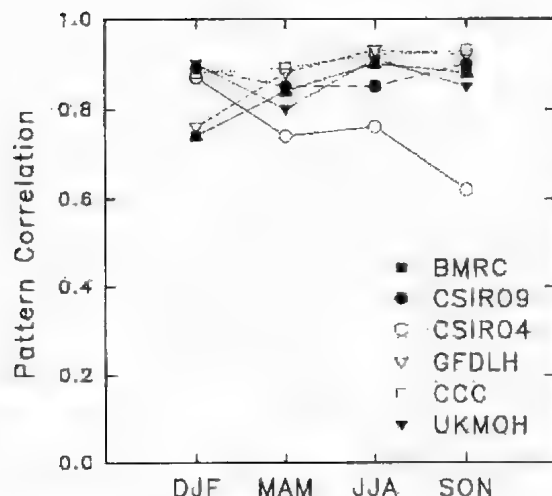


Fig. 4. Pattern correlation for seasonal values of model simulated and observed mean sea level pressure over the Australian region. The abbreviations are for the GCMs and BMRC, CSIRO (4 and 9-levels in the vertical), United States Geophysical Fluid Dynamics Laboratory (GFDL) (High resolution), Canadian Climate Centre (CCC) and the United Kingdom Meteorological Office (High resolution).

representation of the real world. Oceanic GCMs have a similar structure to those described for the atmosphere, but must represent a more "sluggish" fluid with spatial and temporal scales of processes and interactions that are slower than in the atmosphere. It must also be remembered that models of the atmosphere owe much to a long history of scientific endeavour to improve weather forecasts. Oceanic model technology has lagged behind and these models require considerable further development. Much of this is due to sparse observational data coverage for the oceans, which limits the validation of model output, and the need to resolve smaller scale processes involving meso-scale eddies in order to achieve more realistic simulations. The status of coupled model development at the Australian Bureau of Meteorology is given in Power *et al.* (1993). Similar development at CSIRO's Division of Atmospheric Research is in a rather more advanced state.

In using GCMs for studying variations or changes in the global climate, one important prerequisite is that the models can perform an acceptable simulation of current climatic elements. A number of intercomparisons between various GCM simulations of climatic fields and observed climatic parameters

have now been performed by research groups around the world (Houghton *et al.* 1990, 1992). Specific intercomparisons for GCM simulations over the Australian region are detailed in Whetton & Pittock (1991, 1993) and Whetton *et al.* (1994) (Fig. 4). The most encouraging aspect of these checks, is that they have objectively revealed a general improvement in GCM simulations as model resolution and physics have been refined.

The procedure employed to set up a model run to produce "control" or present climate conditions usually involves an experiment where the GCM is run forward in time under the current atmospheric CO_2 concentration with observed sea surface temperatures and initial atmospheric input fields. The aim of this type of experiment is to obtain a sample of simulated climate long enough for statistically valid analysis. In practice, this normally requires between 10–30 years of simulated climatic variables. The various fields generated can then be examined using careful statistical techniques that check the pattern of correlations between each of the GCM control output data distributions with the appropriate observed field patterns. Simulated fields can also be examined for grid point and total spatial field significance. If this proves to be satisfactory, then the GCM can be used to address the possible change in climate that could result from the enhanced greenhouse effect.

Two types of experiments are commonly conducted to assess possible climatic change due to increasing CO_2 . The first, and most widely employed technique is one in which the experiment is performed by simply running the GCM with doubled CO_2 . These equilibrium simulations require about a 10-year time period for the GCM to adjust to the new CO_2 limit after it is instantaneously imposed, and then a sample of the next 20–30 years of data is taken to represent the enhanced greenhouse climate statistics. A doubling of CO_2 is a standard experiment used as a benchmark against which all GCMs can be compared. It does not refer to any particular date in the future and implicitly includes the radiative effect of increases in other greenhouse gases, which are expressed as CO_2 -equivalents. The more physically realistic approach, which is being undertaken as coupled ocean-atmosphere models become more widely available and computing capabilities improve, is to perform a transient experiment. In this type of simulation the CO_2 in the model atmosphere is gradually increased in a manner which loosely approximates the projected increases in this gas, in a time when the level has doubled.

International evaluations of climate change research and GCM simulations and intercomparisons are compiled in the reports of the Intergovernmental Panel on Climate Change (IPCC) (Houghton *et al.* 1990, 1992). In Australia, GCM research with "in house"

models is concentrated at BMRC and CSIRO Division of Atmospheric Research. Both groups have produced doubled CO_2 equilibrium runs using improved versions of their GCMs, and are developing GCMs for transient experiments (Power *et al.* 1993) and to simulate ENSO and natural climatic variability. At the CSIRO Division of Atmospheric Research, results of enhanced greenhouse effect experiments have been used as part of the input into regional climate change scenarios for Australia. Important contributions to IPCC evaluations have been made by CSIRO's Division of Atmospheric Research through studies examining the resolution of possible changes in rainfall amounts and intensities in doubled CO_2 simulations (Gordon *et al.* 1992). This group also has reported on the nature of variability within the climate system simulated by doubled CO_2 experiments (Gordon & Hunt 1994). Climate variability studies at CSIRO include those using the recent Atmospheric Model Intercomparison Project (AMIP) results to highlight the impact of chaotic influences on the atmosphere (Dix & Hunt 1994) and an ongoing experiment simulating 500 years of climate.

Limited Area and nested modelling

The need to focus on likely changes in regional climates, together with the poor spatial resolution of GCMs, means that models that can resolve smaller scale processes are required. Limited area models (LAMs) have finer spatial resolutions than the GCMs and can resolve features of orography and geography that are smoothed in coarser global models (Giorgi 1990; Giorgi *et al.* 1990, 1992). Typical horizontal grid resolutions that have been achieved by LAMs in Australia are as low as 60 km with 18 levels in the atmosphere (McGregor & Walsh 1993; McGregor *et al.* 1993a). LAMs are constructed to cover limited regions of the Earth's surface and to focus on specific features of the climate system while being computationally economical. Such models can be used to examine how a particular synoptic system, such as a tropical cyclone, may have behaved if it were to have been influenced by different environmental conditions (Evans 1993; Evans *et al.* in press). For enhanced greenhouse experiments this may involve increasing sea surface temperatures to mimic doubled CO_2 conditions and then testing the sensitivity of the tropical cyclone and the amount of rain it produces to such a change in boundary conditions. These models are particularly useful in assessing the sensitivity of local precipitation-producing systems to a changed environment. Joint research by BMRC and DAR has concentrated on the simulation of "east-coast" lows or what are often termed "cut-off" lows that can produce copious rainfall over southeastern Australia. This co-operative study is examining the effect that increased sea surface temperatures may have on the precipitation regime of these synoptic systems (McInnes *et al.* 1992).



Fig. 5 Schematic showing the nesting of the LAM grid within the CSIRO GCM grid over Australia.

An important new development using both GCMs and LAMs is the combination of the two in what is termed a "nested" model. The GCM generates the information from a full global simulation and provides the boundary conditions for the LAM that is embedded or nested within the larger, coarser model. This is illustrated in Fig. 5. The nested modelling approach is capable of resolving features as small as 60×60 km. Recent research at the CSIRO Division of Atmospheric Research has focused on the use of this approach to produce finer scale regional resolution of climatic features and their sensitivity to changed environmental conditions. So far, LAMs have only been nested in equilibrium boundary conditions produced by GCMs with a simple Q-flux corrected ocean model. As such, these LAMs are limited in their performance by the accuracy of the GCM boundary conditions.

Other types of models are currently being used or developed internationally and in Australia. One interesting application is the use of tracer transport models to examine the atmospheric CO_2 budget. Studies at CSIRO DAR using such models are described in Enting *et al.* (1993). Such work is particularly important in helping to estimate the global carbon budget.

Conclusions

Over the last five years, progress in developing numerical computer models of the climate system has been substantial, mainly as a result of the stimulus provided by concern about the enhanced greenhouse effect and the need to investigate its possible global impacts. Today a suite of numerical models is being developed to tackle various problems relating to the climate system. Specialised low order models focusing on particular features of the climate system are best exemplified by models of the ENSO phenomenon. Such research has already been responsible for significant improvements in the forecasting of ENSO phases. Larger atmospheric and oceanic GCMs are used to simulate the global climate and likely changes and fluctuations in climatic patterns due to the enhanced greenhouse effect and natural variability. Efforts are also progressing with the full coupling of the ocean-atmosphere system and the addition of realistic and interactive cryospheric and biospheric elements. Finer-scale resolution in the numerical modelling of climate has been attempted using LAMs that have been nested in the coarser GCMs, or used as "stand alone" models capable of resolving specific synoptic features and their sensitivity to potential changes in the climate system.

Considerable further research is needed to continue such developments and to take the current generation of models to a stage where fully interactive Earth system representations are possible. Such improvements then open up the possibility of simulating the nature of fluctuations and changes in the global climate system more realistically. However, these developments must be linked with research to improve observational data records and understanding of climate dynamics; so that model results can be assessed in their proper context.

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SOME IMPLICATIONS OF PAST CLIMATIC CHANGES IN AUSTRALIA

*By M. A. J. WILLIAMS**

Summary

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An important question, in the context of possible human impact on global climate, is whether past climatic history can offer insights into possible future climatic change. Equally critical is the likely response of the physical environment to any future climatic changes. Evidence from pollen analysis, lake fluctuations, desert dunes and coastal plains from Holocene deposits in Queensland, Victoria, New South Wales and Northern Territory, demonstrates that the response of different elements of the Australian landscape to geologically-recent changes in temperature and precipitation was often time-transgressive. Any attempt to use palaeoenvironmental data to predict possible future change must therefore take due account of the varying response times of different constituents of the Australian landscape to external disturbance. A synchronous response to climate change is more likely with relatively simple biophysical systems such as small closed lake basins or source-bordering dunes than with more complex systems such as tropical rainforests and tropical coastal plains.

Key Words. Climatic change, Australian landscape, past climates, Queensland rainforest, Victorian lakes, New South Wales dunes, Northern Territory coastal plains, response times.

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Introduction

There is increasing concern that the accelerating impact of human activities upon our natural resources of land, air, water, plants and animals is seriously damaging many of our more fragile ecosystems, culminating in irreversible losses of genetic as well as cultural diversity. Human actions may also be contributing to possible changes in world climate through a combination of burning of fossil fuels and changing land use (most notably deforestation), both of which reduced the terrestrial store of carbon by about 6.0 ± 0.5 and 1.6 ± 1.0 PgC in 1990, respectively (Houghton *et al.* 1992).

Although the increase in the atmospheric concentration of carbon dioxide, methane, nitrous oxide and other "greenhouse" gases since the start of the industrial revolution is well documented, the likely impact upon global climate and ecosystems remains unclear (Pearman 1988; Houghton *et al.* 1990; Dunnette & O'Brien 1992). Notwithstanding the unavoidable scientific uncertainties over the magnitude and frequency of future climatic fluctuations, there appears to be a significant measure of agreement that the increase in anthropogenic aerosols and trace gases will enhance the greenhouse effect, culminating in global warming of the lower atmosphere, particularly in middle to high latitudes (Houghton *et al.* 1990; 1992). However, there is far less agreement on how the global pattern of precipitation might respond to enhanced greenhouse warming, prompting a number of researchers to look to the past as a source of possible

analogues for future global warming (De Deckker *et al.* 1988; Petit-Maire *et al.* 1991; Street-Perrott 1994). The aim of this paper is to consider some of the ways in which a study of geologically recent changes in the Australian environment can offer insights into how the various elements of our natural environment are likely to respond to future climatic change.

Past climatic changes

Will climatic history repeat itself?

The search for past climatic analogues of a warmer future planet earth is based on a number of explicit and implicit assumptions. A major but unproven assumption is the notion of cyclic change: "as in the past, so, too, in the future". Linked to this assumption of recurrent climatic changes is the equally unproven assumption of similar recurrent boundary conditions. Boundary conditions in this context means the global distribution of land, sea and ice; the global distribution of major vegetation zones; and the global albedo pattern. Insofar as global fluctuations in surface insolation and in ice volume are linked to cyclical changes in the orbital geometry of the earth at time-scales of 10^4 - 10^5 years, certain climatic changes are indeed cyclic, at least when set against the last two million years of the Quaternary period (Williams *et al.* 1993). But what of time-scales of shorter duration, more obviously relevant to present human preoccupations? Here it is important to distinguish between climatic change and climatic variability.

Climatic change and climatic variability

Much confusion over climatic variability and climatic change stems from a failure to specify the time

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scale involved. Fig. 1 illustrates climatic variability at different time scales during the last 0.9 million years (0.9 Ma) of the Quaternary. From 20 000 to 10 000 years ago (20–10 ka), the trend in global climate was from cold to warm, but relative to the preceding 0.9 Ma, this warming was but one peak in a series of global climatic fluctuations from cold to warm to cold again, repeated at least eight times in the last 0.9 Ma.

It is important to remember that the Little Ice Age (Fig. 1b) affected both hemispheres more or less synchronously. World temperatures have increased in the last hundred years, with a brief return to cooler

temperatures between about 1940 and 1960 (Fig. 1a). None of these global temperature changes seem to be linked in any obvious way to the steady exponential increase in the concentration of atmospheric carbon dioxide – a point conveniently forgotten by over enthusiastic advocates of enhanced greenhouse warming.

The reconstruction of past climatic events

The reconstruction of past climatic events is based on many independent sources of proxy data. These “natural archives” include terrestrial and marine deposits and fossils, as well as evidence from archaeology, isotope geochemistry and archaeology. The temporal resolution, temporal range and type of information which may be gleaned from the proxy data sources are illustrated in Table 1, and are discussed in detail by Bradley (1985, 1990) and by Williams *et al.* (1993).

Limitations of palaeoclimatic enquiry

Certain elementary precautions are essential when using any particular type of evidence to reconstruct past environments and climates. Each may be useful for a particular purpose and for a particular spatial and temporal time-scale. However, as Williams *et al.* (1993) note: “Difficulties arise immediately when we use Procrustean tactics to force the data to yield palaeoenvironmental information at particular scales in space or time for which those data are totally inappropriate. A related issue is the precision available in dating the proxy data or samples used in reconstructing past events” (*op cit.*, p. 9).

Reconstruction of past climates thus requires good chronology as well as careful analysis of appropriate natural archives. Nor must it be forgotten that climate is a second-order concept. First-order interpretation

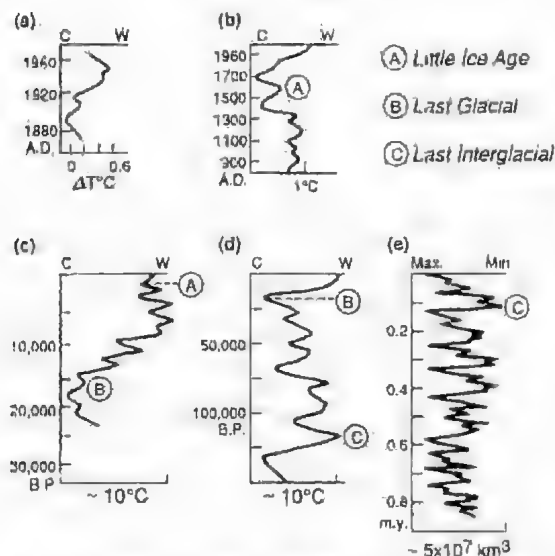


Fig. 1. Climatic variability at different scales in time during the last 0.9 million years (from Williams *et al.* 1993, adapted from Australian Academy of Science 1976).

TABLE 1. Characteristics of natural archives used in palaeoclimatic reconstruction. (After Bradley 1990, Table 1.)

* Minimum sampling interval in most cases. T = temperature; H = humidity or precipitation; C = chemical composition of air (C_a), water (C_w) or soil (C_s); B = biomass and vegetation patterns; V = volcanic eruptions; M = geomagnetic field variations; L = sea levels; S = solar activity.

Archive	Best Temporal Resolution*	Temporal Range (yr)	Information derived
Historical records	day/hr	10^3	T, H, B, V, M, L, S
Tree rings	season/yr	10^4	T, H, C_a , B, V, M, S
Lake sediments	tr to 20 yr	10^4 – 10^6	T, H, C_w , B, V, M
Ice cores	yr	10^5	T, H, C_a , B, V, M, S
Pollen	100 yr	10^5	T, H, B
Loess	100 yr	10^6	H, B, M
Ocean cores	1000 yr	10^7	T, C_w , B, M
Corals	yr	10^4	C_w , L
Paleosols	100 yr	10^5	T, H, C_a , V
Geomorphic features	100 yr	10^7	T, H, V, L
Sedimentary rocks	yr	10^7	H, C_s , V, M, L

of a natural archive usually provides direct information about some component of the natural environment, such as a river, lake or dune. To infer climate (or some particular attribute of climate, such as temperature or precipitation) from a particular element of the landscape is a far more circuitous and difficult procedure, with far greater scope for interpretative error.

Consider, for instance a lake. The outstanding work by Gasse, Fontes, Street-Perrott and co-workers on reconstructing the climatic history of lakes in Africa has demonstrated the need for calibration using present-day chemical, physical and biological data, as well as the need for taking due account of local hydrological factors and of extreme events when deducing palaeohydrology from palaeolimnology (Fig. 2) (Street-Perrott & Roberts 1983; Fontes *et al.* 1985; Gasse *et al.* 1987; Street-Perrott 1991). Only then is it possible to attempt a reconstruction of palaeoclimate. From reconstruction of local palaeoclimates to regional or even global palaeoclimatic modelling is yet another step removed from the original field data. Provided that the limitations of palaeoclimatic enquiry are clearly recognised, and the appropriate steps are followed in interpreting past climate from proxy data, useful insights are possible when using past environmental analogues.

Past environmental analogues

A decade has elapsed since Pittock & Salinger (1982, 1983) suggested that the early Holocene climate of Australia towards 9000–7000 years ago may be a suitable analogue for the continent in a CO₂-warmed earth. Granted that many early Holocene lake and

pollen sites in Australia and Papua New Guinea do seem to indicate a warmer and/or wetter climate at this time (Williams 1984), just how reliable is the evidence? Can it be quantified? Is the "Climatic Optimum" or "Hypsithermal" in Australia indeed a valid analogue of future warming? Finally, can we glean anything else of value to future climate prediction from the record of early Holocene environmental change in Australia?

In an attempt to answer some of these questions, it is appropriate to consider the evidence from a variety of different Holocene sites across Australia. In the ensuing discussion we consider four distinct types of Holocene site in four widely separated localities: the rainforests of northeast Queensland, "maar" lakes of western Victoria, the source-bordering dunes of central western New South Wales, and the coastal plains of the Alligator Rivers area in Northern Territory.

The Holocene rainforests of northeast Queensland

Kershaw's (1983) palynological studies of the late Pleistocene and Holocene vegetation history at four pollen-bearing lake or swamp sites in the Atherton Tableland of northeast Queensland have revealed that the period of maximum rainforest expansion lasted from 6000–8000 to 3000 years B.P. (Fig. 3).

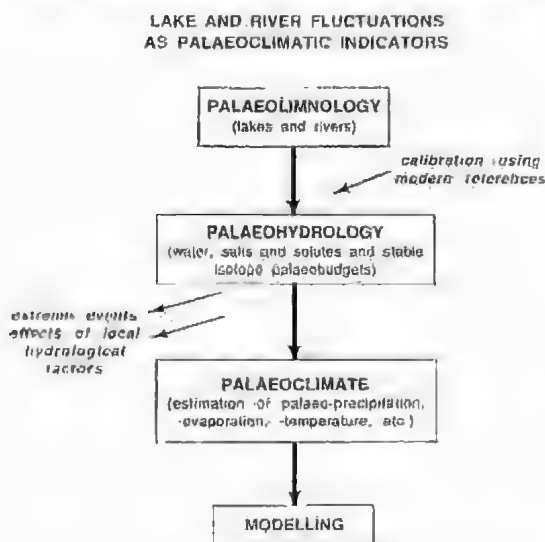


Fig. 2. Lake and river fluctuations as palaeoclimatic indicators (Source: P. Gasse 1986, unpublished seminar paper to Department of Geography, Monash University).

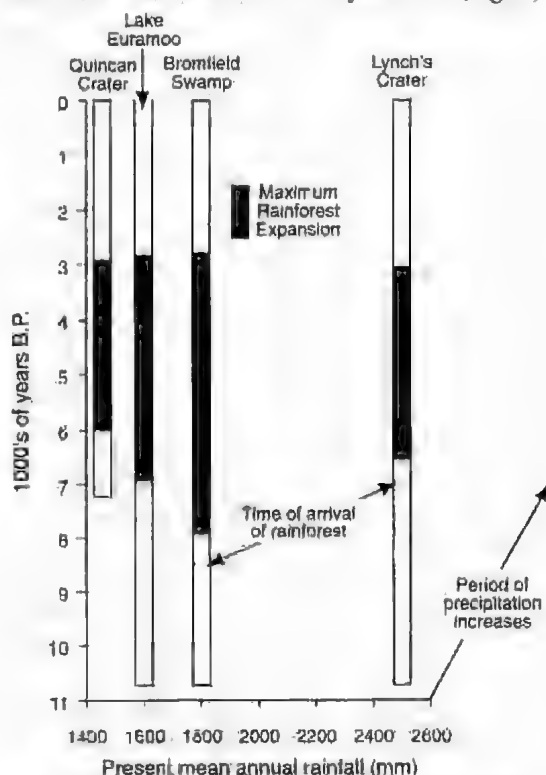


Fig. 3. Vegetation changes in northeast Queensland deduced from pollen analysis of Holocene crater lake sediments. (From De Deckker *et al.* 1988, adapted from Kershaw 1983.)

However, as Figure 3 clearly shows, the response of the rainforest to increasing warmth and increasing effective precipitation was strongly time-transgressive. Rainforest appears in the Bromfield Swamp pollen record towards 8500 years B.P., at Lake Quincan Crater not until after 7000 years B.P. The demise of the rainforest at all four sites was roughly synchronous (3000 years B.P.), indicating that the rainforest responded slowly to climatic amelioration (warmer and wetter conditions) but rapidly to climatic deterioration (cooler and drier conditions).

Application of the CSIRO bioclimatic prediction system developed by H. A. Nix to Kershaw's Queensland rainforest pollen data enabled Kershaw & Nix (1989) to derive more quantitative estimates of the Holocene climates. Their analysis revealed that Holocene temperature maxima were not achieved in the Atherton Tableland until 5000 years B.P., with mean annual temperatures up to 3.5° higher than today persisting until about 3500 years B.P. Mean annual precipitation at that time appears to have been at least 300 mm higher than today, and most probably 500-800 mm higher (Kershaw & Nix 1989; De Deckker *et al.* 1988).

One obvious conclusion to be drawn from the

Queensland pollen record is that the interval 7000-9000 years B.P. was not the time of "Climatic Optimum" for northeast Queensland. The wettest and warmest period came considerably later, and on present evidence seems to have lasted from 5000 to 3500 years B.P. If this is true for the tropical northeast of Australia with its monsoonal summer rainfall regime is it true also for the temperate southeast of the continent, where the rainfall comes mainly from the westerly airmasses which pass across the southern margins of the continent most persistently in winter, when the Antarctic convergence is in its most northerly position?

The Holocene crater lakes of western Victoria

Lake Keilambete in Victoria is perhaps the best studied Holocene lake in Australia (Dodson 1974; Bowler 1981; De Deckker 1982; Chivas *et al.* 1985; 1986). Like other volcanic explosion-crater or "maar" lakes in Victoria, it occupies a small closed basin and is highly sensitive to changes in precipitation and evaporation over its catchment. Five "maar" lakes in western Victoria, including Lake Keilambete, have yielded useful information about Holocene changes in the balance between precipitation and evaporation (De

P/E Estimates for 5 Victorian Maar lakes for the Holocene

	Keilambete	Gnotuk	Bullenmerri	West Basin	East Basin
0	Medium and becoming low	Becoming Low - Medium	Becoming Low - Medium	Low	Low ?
1	Medium	Medium	Medium	?	Medium ?
2	Low and changing	Low	Low	Low	Low
3	Low	Medium	Medium - Low	Low - Medium	Medium
4	Medium	Medium	Medium	Medium	
5	High	High	High	High	High
6	High	High	High - Medium	High	
7	Medium	Low	Medium - Low	Low	No record
8	Low	Lowest	Medium	Lowest	
9	Lowest	Lowest			
10					

50 km

Fig. 4. Changes in Holocene precipitation/evaporation (P/E) ratios for five volcanic "maar" lakes in western Victoria. (From De Deckker *et al.* 1988.)

Deecker 1982; De Deecker *et al.* 1988). Highest precipitation/evaporation (P/E) ratios, peak lake levels and lake salinity minima were all within the interval 7000 to 5000 years B.P. From 5000 to 3000 B.P. (when northeast Queensland was warmer and wetter than today) lake levels were lower and salinity values were higher than in the preceding 2000 years or so (Fig. 4).

One possible inference is that winter rainfall may have been lower towards 5000–3000 years B.P. Equally plausibly, total annual rainfall (including both summer and winter precipitation) may have been reduced at that time. We cannot, as yet, choose between these two possibilities. What does appear certain is that the time of greatest effective precipitation (7000–5000 years B.P.) was several thousand years earlier than the time of maximum effective precipitation in northeast Queensland. It is tempting to speculate that we are seeing the effects of two distinctive climatic systems: one (in northeast Queensland) controlled by the tropical summer monsoon, the other (in western Victoria) controlled by the winter westerlies. If so, the response of both systems to postglacial warming was not synchronous along the eastern third of Australia. Nor may it be synchronous in the face of any future global warming. We turn now to the semi-arid inland areas of New South Wales.

The Holocene source-bordering dunes of central western New South Wales

Holocene palaeoclimatic data are exceedingly scarce for the semi-arid and arid areas of Australia which together comprise 75% of our present land area. The late Pleistocene fluctuations in the Willandra Lakes region of western New South Wales so carefully dated and elucidated by Bowler (1970¹, 1983) do not yield a Holocene signal and in any event have far more to do with runoff from the Eastern Highlands via the Pleistocene Lachlan-Willandra river system than with local changes in rainfall and evaporation (Williams *et al.* 1986).

One climatically-sensitive area capable of providing useful information about local hydrological events is the desert margin system of central western New South Wales studied by Wasson (1975², 1976) and by Williams *et al.* (1991). The study area occupies about 80 000 km² in the semi-arid region bounded by the Darling River to the north and west, and the Willandra

Creek distributary of the Lachlan River to the south (Fig. 5). There are no perennial rivers in the entire area. The ephemeral stream channel known locally as Crowl Creek or Sandy Creek (Fig. 5) flows intermittently during very wet years and the west to east trending linear dunes are today vegetated and stable.



Fig. 5. Map of central western New South Wales showing location of Sandy Creek. The shaded areas are isolated ranges over 200 m in elevation. (Source: Williams *et al.* 1991).

The Holocene climatic history of this vast area is poorly understood, but the pattern of local environmental changes is now reasonably well documented (Figs 6, 7). Source-bordering dunes were actively forming from channel sands ferried in by Sandy Creek between about 5500 to roughly 600 years B.P. Both before and after that interval the dunes were inactive, vegetated and stable (Williams *et al.* 1991).

Source-bordering dunes are dunes which develop immediately downwind of a parent source of sand, such as the sandy bed of a river, a sandy lake beach or a sandy alluvial fan. There are three prerequisites for the formation of source-bordering dunes:

- (1) A regular replenishment of the sand supply (for instance, from a seasonally-flowing sand-bed channel).
- (2) Strong unidirectional winds for at least part of the year; and
- (3) A sparse or limited vegetation cover adjacent to the sand source.

Any interpretation of the Holocene climatic history of this region must take into account the requirements for source-bordering dune formation, the apparent absence of early to middle Holocene dune deposits in

¹BOWLER, J. M. (1970) Late Quaternary environments: a study of lakes and associated sediments in southeastern Australia. Ph.D. thesis, Australian National University, Unpubl.

²WASSON, R. J. (1975) Evolution of alluvial fans in two areas of southeastern Australia. Ph.D. thesis, Macquarie University, Unpubl.

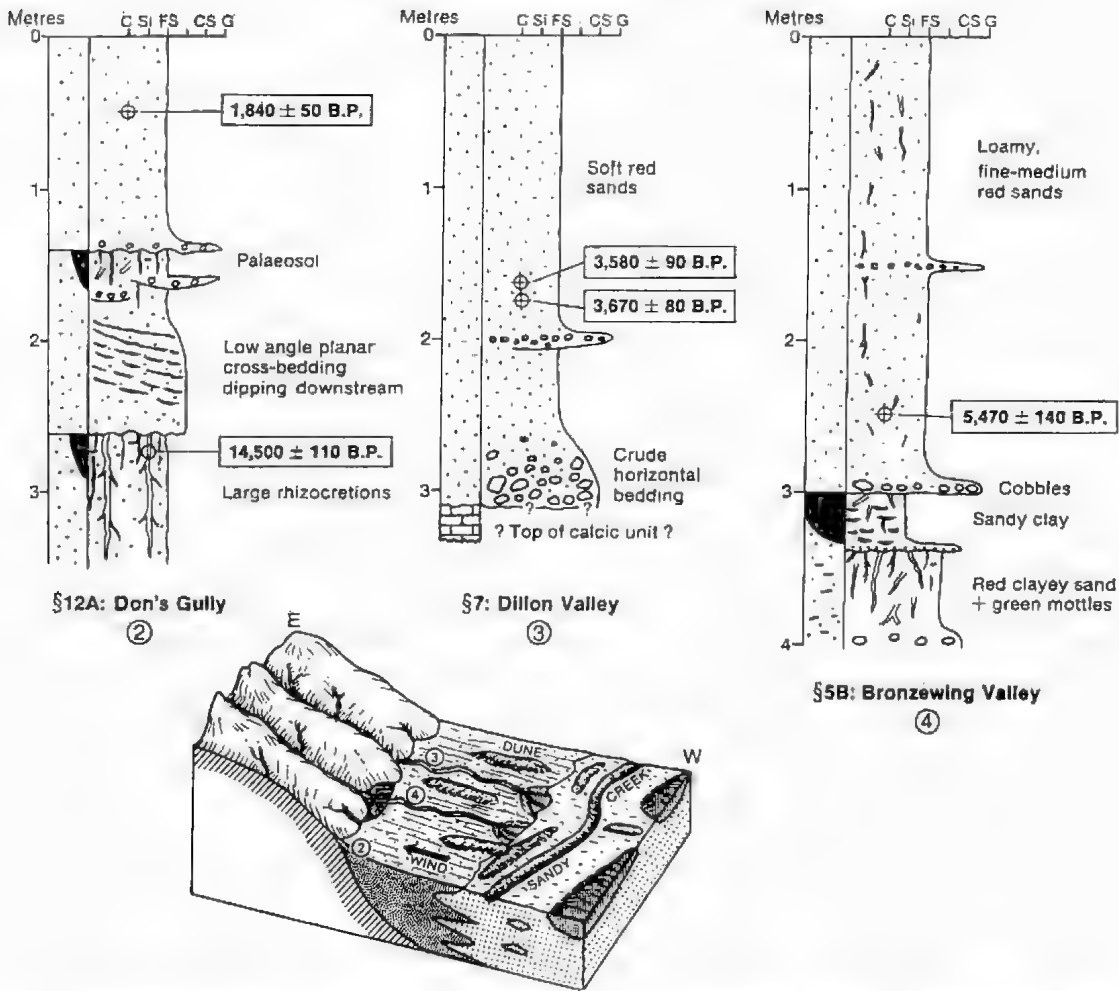


Fig. 6 Representative alluvial fan stratigraphic sections exposed in the gullied western piedmont of Belarabon Range (see Fig. 5). The block diagram shows Sandy Creek, the source-bordering dunes and the wind direction. (Source: Williams *et al.* 1991).

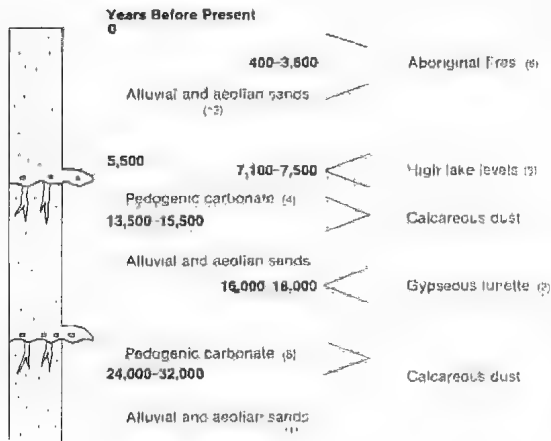


Fig. 7. Generalised late Quaternary piedmont stratigraphy in the central western New South Wales study area. The numbers in brackets denote numbers of samples dated, and includes both radiocarbon and thermoluminescence dates (Source: Williams *et al.* 1991, revised to show additional dates.)

this area (Fig. 7), and the fact that the present-day dunes are vegetated and stable, A tentative palaeoclimatic interpretation, based mainly upon the geomorphic evidence and needing to be tested by future independent work, is as follows:

• 10,000-5500 years BP:

Rainfall more uniform
Wind velocities low
Surface well vegetated
Erosion and deposition very slow

• 5500-600 years BP:

Higher winter rainfall
Seasonal channel flow
Summers very hot, dry and windy
Summer deflation

• 600 years B.P. to present:

Hot summers, cold winters
Rainfall more uniform
Wind velocities low and/or
Denser vegetation

If this interpretation is correct, any change to a wetter climate or to a more seasonal distribution of rainfall, with more runoff during the winter months, could lead to a renewed phase of source-bordering dune formation provided the summers remained dry and windy and the riparian vegetation relatively sparse. Should the future climate in this area become both warmer and wetter, the somewhat paradoxical outcome could be a replenished sand supply and reactivation of the linear source-bordering dunes.

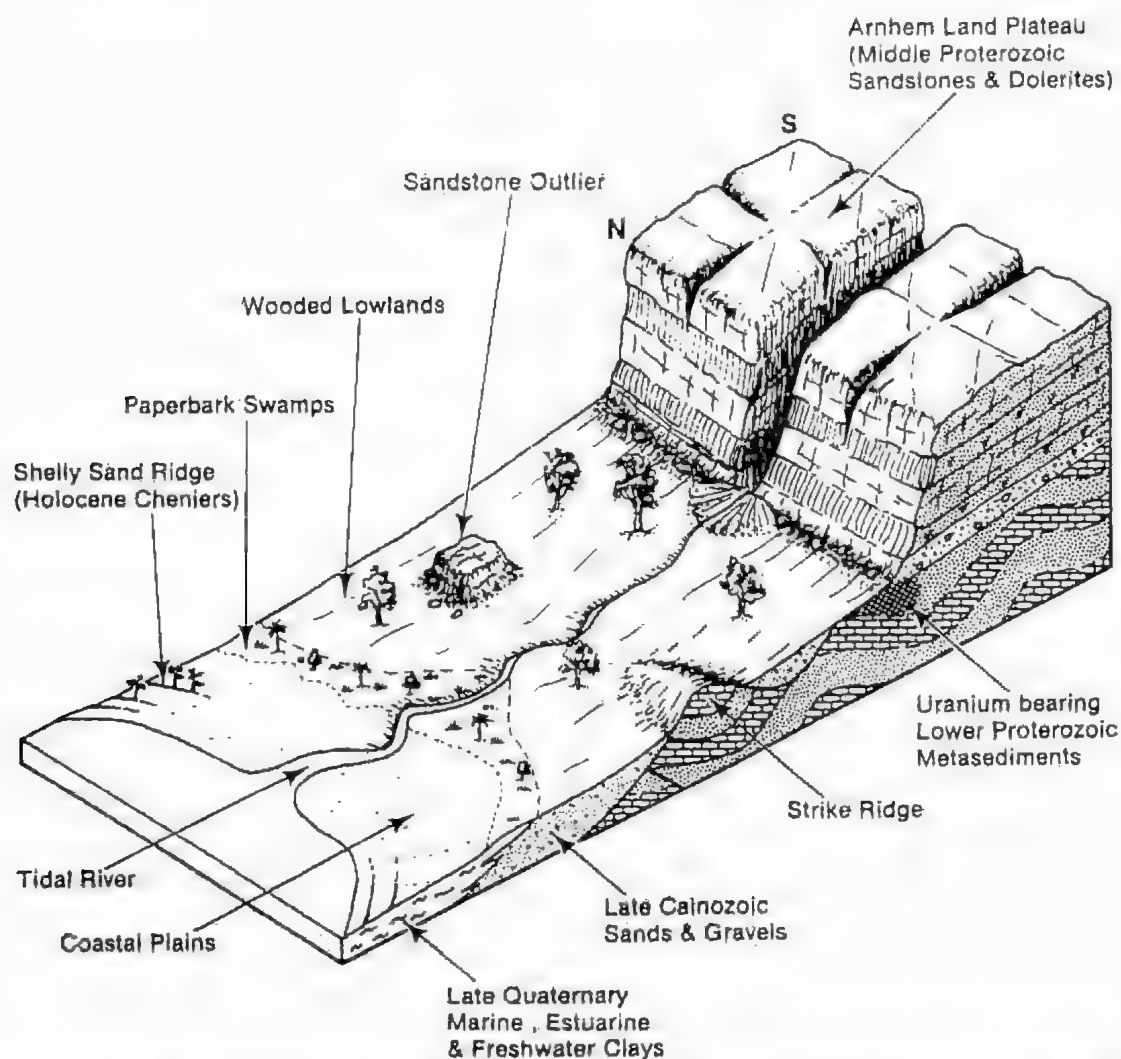


Fig. 8. Block diagram showing the Arnhem Land plateau of Northern Territory and the geologically youthful coastal plains to the north. (Source: Williams 1991.)

The Holocene coastal plains of the Alligator Rivers area, Northern Territory

The tropical coastal plains of Northern Territory stand in almost diametric contrast to the ephemeral streams and desert dunes of semi-arid western New South Wales. Their significance stems from the fact that the Holocene coastal plains which extend for some thousands of kilometres from the far northwest of Western Australia to the far northeast of Queensland are very dynamic landforms, and highly sensitive to even minor changes in sea level, sediment load, salinity and wave climate (Williams 1991). They are also host to a unique and abundant fauna and flora (Haynes *et al.* 1991). In addition, the coastal plains west of Darwin abut onto the Arnhem Land plateau (Fig. 8), with its abundant galleries of Aboriginal rock art, and its record of over 50 000 years of prehistoric Aboriginal settlement (Roberts *et al.* 1990).

With the melting of the late Pleistocene ice sheets of North America and Europe, world sea levels rose from their last glacial maximum level of about -35 m (at 18 000 years B.P.) to their present levels towards 6000-7000 years B.P. (Williams *et al.* 1993).

The initial rise was rapid, and vast areas of the continental shelf off northern Australia were submerged at a rate of over 20 metres a year or roughly 40 cm a week. Once this rise had slowed down, which it did in the last few thousand years, coastal mangroves began to colonise the intertidal muds, allowing muddy sediments to accumulate on the old late Pleistocene land surface inland of the coastal mangrove fringe. This process accelerated once the sea attained its present level, and widespread mangrove swamps developed across the present area of the coastal plains in mid-

Holocene times, from about 5000 to 2000 years B.P. (Woodroffe *et al.* 1985). These mangrove swamps proved to be highly efficient sediment traps, and were eventually buried by estuarine and, ultimately, by freshwater muds (Woodroffe *et al.* 1986; Williams 1991; Wasson 1992). The present-day coastal plains are thus a relatively youthful feature, and are generally less than 2000 years' old.

How these plains might respond to sea level change will depend upon a variety of factors, including the rate of sea level rise; the impact of any climatic change upon runoff and sediment yield in the tidal rivers; the magnitude and frequency of future cyclones, and the relative duration of the wet and dry seasons. Since none of these variables is accurately predictable, speculation seems unwarranted beyond noting that the coastal plains are likely to remain a geomorphically dynamic and actively developing feature of the landscape, just as in the past 5000 years.

Conclusion

Provided certain common-sense precautions are observed, an appreciation of Holocene climatic and other environmental changes in Australia can be a useful guide to possible future landscape responses to global warming whatever its ultimate causes. The Australian landscape is a palimpsest of landforms, soils and plant associations, all of which will respond to future climatic change in a variety of ways. The way in which our rainforests, lakes, dunes and coastal plains have responded to Holocene climatic changes offers us some guide to their possible future responses. It is highly unlikely that these will be either simple or synchronous.

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CLIMATE CHANGE AND ITS IMPLICATIONS FOR SOUTH AUSTRALIAN SOILS

BY R. W. FITZPATRICK† & M. J. WRIGHT**

Summary

Fitzpatrick, R. W. & Wright, M. J. (1994) Climate change and its implications for South Australian soils. *Trans. R. Soc. S. Aust.* 118(1), 27-34, 31 May, 1994.

The nature and distribution of dominant soils in South Australia is briefly reviewed with particular reference to major issues relating to climate change. For this purpose the State has been divided into two regions: (i) the southern regions or agriculturally developed area which lies south of latitude 32°S and is mainly used for dryland cereal/sheep production and (ii) the northern region or semi-arid and arid areas which mostly lie north of latitude 32°S and are mainly used for low intensity grazing of natural rangeland. A large proportion of South Australia, including many texture contrast soils of the high rainfall areas, has dispersive soils subject to sodicity and which are highly prone to waterlogging and salinity throughout a significant proportion of the profile.

Key Words: climate change, soils, South Australia, soil moisture, soil temperature, soil organic content, salinity, sodicity, soil acidification.

CLIMATE CHANGE AND ITS IMPLICATIONS FOR SOUTH AUSTRALIAN SOILS

by R. W. FITZPATRICK*† & M. J. WRIGHT*

Summary

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The nature and distribution of dominant soils in South Australia is briefly reviewed with particular reference to major issues relating to climate change. For this purpose the State has been divided into two regions: (i) the southern region or agriculturally developed area which lies south of latitude 32°S and is mainly used for dryland cereal/sheep production and (ii) the northern region or semi-arid and arid areas which mostly lie north of latitude 32°S and are mainly used for low intensity grazing of natural rangeland. A large proportion of South Australia, including many texture contrast soils of the high rainfall areas, has dispersive soils subject to sodicity and which are highly prone to waterlogging and salinity throughout a significant proportion of the profile.

This paper attempts to forecast the most likely consequences of global climate change on the dominant soils of South Australia. The direct influence of increasing winter temperatures and decreasing winter rainfall on the wide range of soil types that occur in South Australia is as yet unclear. However, the magnitude and extent of supposed degradation or enhancement of particular soil morphological properties, and decline or increase of soil site properties (e.g. salinity or erosion) are matters of speculation. In fact, these changes can affect the processes of global climate change by affecting production of greenhouse gases or causing changes in vegetation. How soils modify under the influence of changing climate will depend principally on soil type, topography and changes of vegetation.

South Australia's soils will respond to global climate change through changes in soil moisture, soil temperature and soil organic matter content. Decline in winter rainfall in the high rainfall regions occurring to the south of latitude 32°S will have a beneficial effect by substantially reducing seasonal waterlogging and formation of aqueic soils (including non-tidal acid sulfate soils). In contrast, dryland salinity may continue to expand with a corresponding decline in stream water quality.

It is not yet possible to accurately quantify regional soil changes resulting from climate change given the present uncertainty about the amounts and rates of global climate change, and particularly concerning regional patterns of temperature, precipitation and coastal geomorphic changes. The currently increasing rate of land and water exploitation in South Australia will likely have a greater impact on soils, adverse or beneficial, than the effects of climate change.

KEY WORDS: climate change, soils, South Australia, soil moisture, soil temperature, soil organic content, salinity, sodicity, soil acidification.

Introduction

The greenhouse effect is the warming of the earth resulting from increases in the concentration of carbon dioxide (CO₂) and other radiatively active gases including methane (CH₄), nitrous oxide (N₂O), ozone (O₃) and the chlorofluorocarbons (CFC's) that reduce the loss of outgoing infrared radiation (i.e. limit heat losses from earth into space; Table 1). A global increase in CO₂ has been reliably documented during the last 100 years and although this is due mainly to the burning of fossil fuels there is an appreciable flux of CO₂ from the oxidation of soil organic matter and the burning of forests (Table 1). CO₂ levels of twice the present are forecast by the year 2050 (Pearman 1988; Houghton 1990; van Breemen & Feijtel 1990). Soil is not only a source of CO₂ but also of CH₄ and N₂O (Table 1). Atmospheric warming of about 0.5°C

has been estimated over the last 100 years; estimates of warming up to 5°C over the next 100 years have been made (Bouwman 1990). A corresponding warming of the oceans and rise of sea level of up to 0.5 m are also forecast. Changes of this magnitude and rate represent a significant change in our environment that would have a profound effect on the Earth's ecosystems and human activities (Bolin *et al.* 1986; Wild 1993).

Much of the emphasis in recent discussions of the impact of greenhouse induced climate change in Australia has focussed on the atmosphere and on agricultural and forestry production (Pearman 1988). However, the effects of climate change on Australian soils is also a fundamental issue. Given the present state of severe soil degradation in Australia (e.g. Chartres *et al.* 1992) the possibility of further degradation should be of national concern.

South Australia is a region which is currently influenced mainly by winter rainfall but where the current rainfall varies greatly from north to south. Hence, for discussion purposes, we have divided South

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TABLE 1. Atmospheric concentrations, increase, residence time, sources and sinks for major greenhouse gases, and their contribution to global warming (adapted from Wild 1993; Bouwman 1990; Standing Committee on international programmes of the international society of soil science, 1990).

	CO ₂	CH ₄	N ₂ O	O ₃	CFC's
Residence time (yr)	100	8-12	100 200	0.1-0.3	65-110
Annual increase (%)	0.5	1	0.2-0.3	2.0	3.0
Concentration in 1985	345 ppmv	1.70 ppmv	300 ppbv	na	0.18-0.28 ppbv
Radiative absorption per ppm of increase	1	32	150	2000	>10,000
Contribution (%) to global warming	56	19	4	8	15
Total source	6.5-7.5 Gt C	400-640 Tg CH ₄	11-17 Tg N	—	—
Biotic sources (%)	20-30	70-90	90-100	—	—
Major sources (Gt or Tg)	fossil fuel (5.7) deforestation (1-2)	paddies (60-140) wetlands (40-160) ruminants (65-100) termites (10-100) landfill sites (30-70) oceans/lakes (15-25) biomass burning (50-100) fossil fuel (50-95)	cultivated soils (37) natural soils (?) fossil fuel (?)	atmospheric	manmade
Sinks (Gt or Tg)	atmosph. accum. (3.5) oceans (<1) biosphere (?) charcoal (?)	atmosph. accum. (50) soil oxidation (32) atmosph. chemistry (300-650)	atmosph. accum. (2.8) atmosph. chemistry (10.5) Soils (?)	atmosph. accum. atmosph. chemistry	atmosph. accum. atmosph. chemistry
Net imbalance	1.6				

Australia into the following two regions: (i) the southern region – the agriculturally developed area which lies south of latitude 32°S and is mainly used for dryland cereal/sheep production and (ii) the northern region – the semi-arid and arid areas which mostly lie north of latitude 32°S and are mainly used for low intensity grazing of natural rangeland. The greenhouse effect is likely to influence the soils in each region differently. The southern region is considered likely to suffer a drying climate due to a reduction in winter rainfall whereas the northern region is more likely to receive enhanced summer rainfall. The objectives of this paper are to: (i) summarise existing information on soils in South Australia, (ii) highlight the most likely consequences of global climate change on the range of South Australian soils and (iii) identify future priorities for research on global climate change on South Australian soils.

Soils

Soils are complex systems which are strongly influenced by processes occurring in the atmosphere, biosphere, hydrosphere and lithosphere (Fig. 1).

In general, soils develop slowly over thousands of years, the absolute rates depending to a large extent on past climates. Their component parts also differ in their rates of development. For example, soil biotic processes resulting from the interaction of the atmosphere and biosphere are much more rapid than soil weathering processes resulting from the interaction of the hydrosphere and lithosphere. Thus, in response to greenhouse induced climate change, the more environmentally sensitive soil biotic processes would be expected to respond more rapidly (Bouwman 1990; Varallyay 1990; Wild 1993). In coastal landscapes, many soils would also suffer relatively rapid water erosion, waterlogging and salinisation as sea levels rise with global warming.

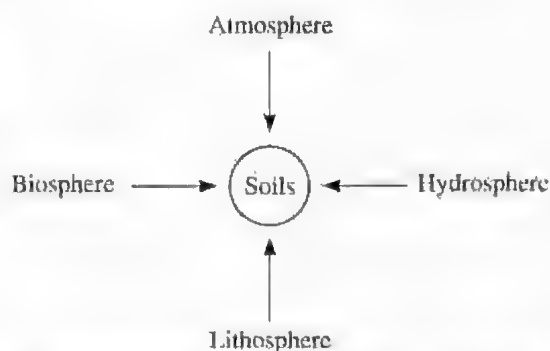


Fig. 1. Simplified diagrammatic representation illustrating that soils are complex systems which are influenced by processes from the atmosphere (climate), biosphere (vegetation and fauna), hydrosphere (hydrology) and lithosphere (geology and topography).

Influence of land clearing

An important factor in assessing greenhouse effect is the change already brought about to Australian soils as a result of European settlement. Land clearing, grazing and cultivation generally have resulted in a rapid decline of soil organic matter and organisms and consequently a deterioration of soil structure and increasing susceptibility to erosion. A marked reduction in the diversity of fauna and flora of most ecosystems has also accompanied European settlement and this has made our soils and landscapes less resilient to change.

The effects of greenhouse induced climate change, therefore, must be assessed for soils and landscapes already degraded: pristine conditions are virtually non-existent. Given this scenario, there is a significant environmental question to be answered: If there is greenhouse induced climate change of the magnitude forecast, what will be its effects on South Australian soils and landscapes?

Soil Carbon and the CO₂ cycle

The amount of carbon stored in the world's soils as fresh organic matter, stable humus and charcoal, is two to three times higher than carbon stored in natural vegetation and crops (Table 1, Bouwman 1990; Standing committee on international programs of the International Society of Soil Science 1990; Wild 1993).

Distribution and major properties of soils in South Australia

Generally speaking, South Australian soil landscapes are extremely variable and complex due, in part, to the great age of much of the continent. A significant proportion (>60%) of soils in South Australia are saline, or sodic and/or texture contrast (i.e. duplex — have bleached sandy to sandy clay loam topsoil horizons overlying clayey subsoil horizons that may, or may not be mottled) (Table 2). Sodic duplex soils are inherently subject to waterlogging because of water

perching on the more impermeable clayey subsoil horizon and consequently saturating the topsoil horizons, especially where there is an increased input of water following removal of native vegetation. A similar effect can be caused, in the short term, by excessive irrigation. Therefore, to proceed from a more general understanding of the processes of waterlogging and dryland salinisation to a more definite understanding of these processes in an individual catchment, in order to predict the effects of management or climate change, is extremely difficult. The central and southern Mt Lofty Ranges area is further complicated by highly variable geology and weathering patterns of the soils in those landscapes. It is apparent that in adjacent landscape positions one is confronted with deeply weathered soils which contain ancient stored salt, juxtaposed with very youthful soils on partly weathered rocks which are generating salt as a result of contemporary weathering processes.

The higher rainfall areas (i.e. greater than 500 mm average annual rainfall) which lie south of latitude 32°S are restricted to coastal and sub coastal plains and ranges. A high proportion of both regions has soils which are sodic throughout or through a significant proportion of the profile. Table 3 lists the estimated areas of sodic soils in South Australia, south of latitude 32°S. The names used represent general profile characteristics that may each include several great soil groups. This has been done to reduce the table to manageable proportions suitable for reproduction here. The semi- and arid regions north of this latitude contain even more significant areas of saline and sodic soils, particularly the desert loams and associated red clays. The table was prepared by re-interpreting maps published by Northcote (1960) and Northcote *et al.* (1968), Sheets 1 and 10, respectively, of the Atlas of Australian Soils; the original scale of which was 1:2 000 000.

TABLE 2 *Distribution of saline and sodic soils in relation to rainfall in South Australia (after Northcote & Skene 1972).*

Annual Rainfall (mm)	Area (km ²)	Saline Soils	Percentage area of each map unit within annual rainfall zones			Non-alkaline sodic		Total (%)
			Alkaline strongly sodic	Uniform texture		Gradational texture	Duplex profile	
							Neutral duplex	Acid duplex
<150*	450,215	25.9	6.9	18.7	—	—	—	—
150-250**	351,910	11.1	1.8	47.0	—	—	—	—
250-350***	82,570	2.3	1.1	59.8	7.5	—	—	—
350-550***	72,745	—	1.5	22.4	34.8	4.2	—	—
>550***	25,560	1.2	9.1	—	24.2	5.9	2.8	—
Total	983,000							

* All within northern region of South Australia.

** Largely within northern region but a significant area of southern region included.

*** All within southern region except for small area of northern region in 250-350 zone.

On an area basis two broad groups of sodic soils are prominent in the southern region, the grey-brown calcareous loams (36% of the area) and the duplex soils with alkaline soil reaction trend (18%), that is, soils with pH generally increasing with depth and alkaline in the subsoil. These two soil groups include the majority of the cereal and sheep producing land in the State. Although of much smaller area, the sodic duplex soils of southern Eyre Peninsula, Yorke Peninsula, the Mid-North, eastern Mt Lofty Ranges, Kangaroo Island and the South-East are critically important because they have high rainfall and a high production potential. They are also important because they indicate the regions where waterlogging and secondary salinisation is a current or potential problem.

TABLE 3. Estimated areas of soils in South Australia south of latitude 32°S (modified after Naidu *et al.* 1993).

	Area km ²	%
Soils that are sodic throughout:		
a) Clayey soils, uniform texture profiles.	3450	1.6
b) Grey-brown calcareous loams, uniform and gradational texture profiles.	75660	36.1
c) Alkaline duplex soils	5335	2.7
Sub-total	84445	40.4
Soils that have sodic subsoils		
d) Alkaline duplex soils	38685	18.5
e) Neutral duplex soils	6185	2.9
f) Acidic duplex soils	2930	1.4
Sub-total	47800	22.8
Total sodic soils	132245	63.2
Non sodic soils:		
g) Alkaline duplex soils	2947	1.4
h) Neutral duplex soils	1893	0.9
i) Acidic duplex soils	5682	2.7
j) Clayey soils, uniform texture profiles	1683	0.8
k) Grey-brown calcareous loams, uniform and gradational texture profiles.	44212	21.0
l) Sandy soils including podzols	21058	10.0
Total non sodic soils	77475	36.8
Land area south of latitude 32°S	209720	100.0

Projections for climate change

Forecasts of greenhouse induced climate change are based on global models that incorporate the circulation of the Earth's atmosphere and oceans and the albedo effect of its polar ice caps. Present models vary in their forecasts of global CO₂ and temperature changes although a commonly accepted view is that a doubling of CO₂ will result in a temperature rise of 4°C (Pearman 1988; Wild 1993). These models also predict, to varying degrees, a consequent increase in

evaporation and precipitation i.e. an intensification of the hydrological cycle with increased rainfall erosivity. Greater uncertainties exist in the prediction of regional climate change and its consequences within continents.

In Australia, a "best guess" scenario has been developed by Pittcock & Nix (1986) based on historic records and a global model from which a rise of between 2 and 4.7°C in mean annual temperature by the year 2030 is predicted (see also Pearman 1988). In summary, temperature increases are predicted to be greatest in southern Australia, particularly in winter; summer rainfall areas will receive an increase in precipitation of up to 50% and the monsoonal influence will extend farther south; the winter rainfall areas of southern Australia will receive less precipitation, particularly in winter.

The climatic models vary even more widely in their prediction of the moisture status of Australian soils under doubled atmospheric CO₂. Only a broad generalisation of increased soil moisture in the north and a decrease in the south can be made.

The uncertainties in predictions of climate change into the next century are considerable. Nevertheless, it is clear that even a modest greenhouse effect will significantly change the regional climatic regimes of Australia. In the southern parts of the continent, particularly, the climate change forecast will create drier soil moisture conditions and impose further limitations for a range of land uses. When this scenario is superimposed on the present pattern of soil degradation in South Australia, it is apparent that large areas of land could be at risk of further degradation.

Not all the predicted consequences of the greenhouse effect, however, are negative. Forecast increased precipitation in the northern part of South Australia would have the potential to increase soil moisture stores with a positive outcome for soil stability and for the pastoral and agricultural industries. In contrast, decreased precipitation in the higher rainfall areas of southern South Australia would reduce seasonal waterlogging (see below).

Impact of past climate change

Because soils and landscapes develop over long periods, many are found to contain information about past climate change. Among the most significant examples are the soils and associated sediments of coastal flood plains about Australia (Division of Soils, CSIRO 1983). At the peak of the world's last glaciation 20,000 years ago, sea levels were about 140 m below the present and the Australian coastline was consequently much more extensive. At the end of glaciation, global seas rose rapidly to reach their present level about 6000 years ago. During this rise, ocean waters invaded large areas of coastal land and embayed all coastal rivers. The rivers deposited

sediment in marine and estuarine environments so that, today, their coastal flood plains contain a continuous record of sedimentation. Around Australia, high water tables, high salinity, and sulphates characterise the soils of these flood plains.

TABLE 4. Possible negative modifications of land-use due to changes in temperature, rainfall and windiness in South Australia.

Coastline

Rising sea levels

- wave erosion
- flooding of coastal flood plains
- salinisation of coastal flood plains

Northern Region (Arid and semi-arid zones which mostly lie north of latitude 32°S)

Increased rainfall and erosivity; slightly higher temperatures

- increased risk of landslides
- increased risk of water erosion
- flooding of lowlands

Southern Region (High rainfall zones which lie south of latitude 32°S)

Changed rainfall incidence; increased erosivity; higher temperatures

- lower soil moisture
- decreased vegetative cover
- loss of soil biotic components and organic matter
- deterioration of soil structure
- increased risk of water erosion
- increased salinisation
- deterioration of stream water quality
- increased wind erosion
- drier atmosphere

In such coastal landscapes, the late geological past provides an accurate guide for predicting the consequences of sea level rise resulting from the greenhouse effect. These are increased flooding and an elevation of water tables, and increased salinisation and encroachment of marine and estuarine environments, accompanied by a build up of sulphidic sediments in expanded mangrove swamps (Tables 4, 5). This will lead to the development of greater areas of acid sulphate soils. The area of coastal flood plain actually affected, particularly in the gulf regions of South Australia, would depend on the magnitude of the sea level rise; a special study would be required for reliable estimates.

Rises in sea level also cause widespread wave erosion of coastal soils near shorelines, as well as destabilisation of coastal dune landscapes (Table 4). Much of the evidence for these effects in the late geological past have been covered by the ocean or obliterated. Nevertheless, a significant risk to coastlines around South Australia is apparent (Harvey & Belperio this volume).

TABLE 5. Possible positive modifications in land-use due to changes in temperature, rainfall and windiness in South Australia.

Coastline

Rising sea levels

- flooding and formation of coastal mangrove swamps

Northern Region (Arid and semi-arid zones which mostly lie north of latitude 32°S)

Increased rainfall; slightly higher temperatures

- increased soil moisture
- increased vegetative cover
- reduced water erosion
- increased soil organic matter

Southern Region (High rainfall zones which lie south of latitude 32°S)

Decreased rainfall; higher temperatures

- lower water tables — ground and perched (reduced incidence of seasonal waterlogging)
- decreased soil acidification

The usefulness of the geological record for predicting the effect of greenhouse induced climate change on other Australian soils and landscapes is much less certain. This is because much of the stratigraphic and geomorphic evidence for climate change during the last 20,000 years relates to world-wide (Pleistocene) glacial climates. In Australia, a large part of Tasmania and a small area of the mainland were glaciated, inland lake levels were high, river discharges were higher than the present, large areas of hill slope land were erosionally unstable and eroded sediment filled local valley floors. In central Australia, the dry phases of the late Pleistocene were characterised by extensive movement of sand dunes and the mobilisation of large quantities of dust which was deposited as a clayey mantle over landscapes in eastern Australia. These unstable soil and landscape conditions changed to relative stability as climate warmed during the last 10,000 years (Holocene).

If we use the past as an analogy, the predicted greenhouse warming should be seen as leading to soil formation and, therefore, not expected to result in widespread instability and degradation of soils and landscapes in non-coastal Australia. However, two factors make the present different from the late geological past. First, the rate of climate change due to greenhouse warming is predicted to be much quicker than climate change of the same magnitude in the geological past. Second, most of our soils and landscapes have already been modified following European settlement in such a way as to make them more vulnerable to rapid environmental change. In many parts of South Australia, thresholds of stability have been exceeded, resulting in accelerated waterlogging, salinisation and erosion (Fitzpatrick *et al.* 1992, 1993). If present land use is not responsive

in greenhouse induced climate change, these and other forms of soil degradation are likely to increase, particularly in the southern region where decreased soil moisture would make present land use marginal in some areas.

In this connection, Pittock & Nix (1986) have modelled changes in plant productivity as a result of projected greenhouse induced climate change in Australia. In northern Australia, the positive outcome of the greenhouse effect in increased precipitation and vegetative cover could mean a shift towards an increase in the stability of soils to water erosion. As elsewhere, however, much would depend on land use practices. A decrease in plant production is anticipated in the southern region of South Australia, signalling a decrease in soil vegetative cover and soil biotic activity. It is suggested that these effects would be relatively rapid with a corresponding decrease in soil structural stability and an increased susceptibility to erosion. In southern Australia, therefore, the year 2050 could see a return towards conditions that prevailed in the late Pleistocene given the upper (worst) greenhouse scenario.

Projections for Soils and Landscapes

From the foregoing, it is possible to outline some of the main consequences of greenhouse induced climate change in South Australian soils and landscapes. Although these can only be broadly stated, they have a potential value in identifying like areas of positive and negative outcomes. These are summarised in Tables 4 and 5. It may be argued that some of these projections are alarmist. However, waterlogging, salinisation, acidification, wind and water erosion are already major problems in South Australia and there is no evidence that they are under control (Fitzpatrick *et al.* 1992, 1993, 1994; Naidu *et al.* 1993). Even the conservative "middle scenarios" of greenhouse induced climate change would exacerbate these problems in many areas.

Soil erosion

South Australia has a high proportion of sodic and saline soils (Northcote & Skene 1972; Naidu *et al.* 1993). The sodic:saline ratio of approximately 5:1 ranges between 4 and 10 times that reported for other continents (Szabolcs 1989) and is consistent with the high proportion of sodium present in soil solutions and groundwaters. In South Australia, most sodium affected soils are the result of past inundations by brackish water supplemented possibly by cyclic salt. Thus, in subsoils, chloride is the dominant anion and exchangeable Mg/Ca ratios are high. The incidence of sodicity often coincides with the spatial distribution of duplex soils. This association indicates a pattern of environmental hazard which appears to at least broadly

coincide with many areas under agriculture in the southern region, and substantially limits its productivity. Saline, sodic and sodic duplex soils are often predisposed to land degradation (e.g. Naidu *et al.* 1993; Isbell *et al.* 1983) and, significantly, cover >60% of the South Australian land mass. The effects of adsorbed sodium on clay dispersion are most pronounced in dense alkaline subsoils which comprise over 86% of Australian sodic soils (Northcote & Skene 1972).

The impact of soil sodicity on the environment is a most important land degradation issue in South Australia. Both primary and secondary sodification of soils causes undesirable changes in soil structure, severe hillslope erosion, waterlogging and erosion of downstream watercourses. The associated increase in colloid and nutrient loading of streams also contributes to sedimentation and the consequent loss of reservoir storage capacity, together with serious water quality problems. However, it is the contact of sodium-affected soils with water in the form of rain splash, surface runoff, through flow, natural ground water flow, or that pumped for irrigation from other catchments, which provides the expanded scale on which environmental problems and hazards become most conspicuous (Fitzpatrick *et al.* 1994).

In South Australia generally, climate change is likely to increase the incidence of water erosion (Table 4). Although lower precipitation in the south will generally reduce the rate of water erosion, this is counterbalanced by the less intensive soil conservation influence of poor vegetative growth due to an inadequate moisture supply for plants (exacerbated by an increase in temperature, as well). Lower precipitation and higher temperatures will also lead to increased wind erosion, especially where sandy soils are dominant (i.e. in the semi and northern portions of the southern region). In the northern region, increased summer rainfall is likely to be of higher intensity than at present and is, thus, expected to present a higher erosion risk there too, particularly to the widespread saline and sodic desert loams and red clays of the stony tablelands.

Waterlogging and dryland salinity

Extensive deforestation which followed European settlement in South Australia has contributed to a detrimental shift in the hydrologic balance of many catchments. This has resulted in a rise of perched and saline groundwater tables causing waterlogging and dryland salinity to be a major land degradation problem in South Australia. Over 220,000 ha of land are estimated to be affected by dryland salinity throughout the major agricultural districts at an annual cost to this state of approximately \$25 million in lost agricultural production. The problem is worsening. In particular, there is a growing concern by property holders in the Mt Lofty Ranges over the rapid increase in saline,

structureless acid sulphate soils that are waterlogged and highly prone to water erosion (Fitzpatrick *et al.* 1992, 1993).

Despite an obvious reduction in seasonal waterlogging due to a decline in winter rainfall in high rainfall regions south of latitude 32°S, dryland salinity may continue to expand with a corresponding decline in stream water quality (Tables 4 and 5). According to Sadler *et al.* (1988), the processes involved in such "saline" sodic soil environments, due to reduced winter precipitation, are further complicated by the balance between rates of leaching and recharge. Overall, the consequent reduction of water quality and land capability are, therefore, only products of a complex set of interactions which can occur between the following factors in Mediterranean climates: sodium-affected soils, ambient levels of soluble salts and the temporal flow patterns, spatial distribution, relative contributions and quality of surface water, and through flow and ground water. In particular, the leaching of saline sodic soils with good quality water (i.e. rainwater) also poses a threat to structural stability in buildings, bridges, earth dams and embankments (Fitzpatrick *et al.* 1994).

Soil acidification

In the southern region, a reduction in winter precipitation may decrease downward infiltration and leaching of water and hence lower the rate of soil acidification. Similarly, a decrease in winter precipitation and increase in winter temperatures will discourage heath vegetation which produces acidifying litter (Table 4). In contrast, in those presently high rainfall regions where climate change will cause an increase in summer precipitation, soil acidification may accelerate due to stronger leaching and chemical reactivity (eg carbonate dissolution may occur).

Biological changes including the nutrient regime

Graetz *et al.* (1988) in discussing the implications of climate change for arid zone vegetation stresses the importance of the spatial patterns of soil types. Furthermore, given the importance of this spatial dimension, there is a requirement, as yet not met, for models of vegetation response to plant-available moisture and available nutrients that are specific to the major soil types. Three requirements were identified for forecasting vegetation change. The first was that, because the spatial patterns of soil type are still expected to determine the distribution of vegetation, it is essential that the forecasts of future climatic conditions have a spatial resolution equivalent to that of the mapped soil landscapes.

We consider that much of the carbon stored in South Australian soils is in the form of charcoal due to a long history of burning. With climate change in the directions discussed, it is reasonable to expect that in

the northern regions, biomass, and hence charcoal will increase, whereas in the southern region reduced rainfall will lead to a generally reduced biomass and consequent reduction in the amount of charcoal produced, even though fire frequency could increase because of higher temperatures and lowered moisture.

Conclusions

Changing agricultural practices (that lead to erosion, salinisation, sodification, acidification and waterlogging) make it difficult to monitor the effects of climate change in individual catchments. Special research that takes account of these complications is needed on specific South Australian soil types to quantify regional effects of climate change and to plan strategies to cope with the changes because of implications for the well being of our communities and the environment. It would appear that the dominantly pastoral activities of the northern region stand to benefit by reason of increased summer rainfall at a time when temperatures are suitable for major growth of herbage. Salinity of surface soils, at least, should also be reduced by the increased precipitation (Brinkman & Brammer 1990). In the southern region, on the other hand, agricultural pursuits could be adversely affected by reduced rainfall, although increased temperatures will improve winter growth of cereal crops. Agricultural activities may also be able to expand somewhat in the northern marginal fringe to take advantage of increased rainfall there. Finally, at a time when the demand for good quality water is escalating, the limited understanding of the factors and interrelationships involved in soil and water management may well be further complicated by a changing global climate induced by the "greenhouse effect".

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CLIMATE CHANGE AND ITS HYDROLOGICAL IMPLICATIONS FOR SOUTH AUSTRALIA

By B. C. BATES, S. P. CHARLES*, N. R. SUMNER*, & P. M. FLEMING†*

Summary

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Introduction

Global climate change caused by rising atmospheric concentrations of carbon dioxide (CO_2) and other trace gases may have a significant impact on regional water resources. Recent research suggests that plausible climatic changes will affect the timing and magnitude of runoff and soil moisture, change lake levels, and increase evapotranspiration (Cohen 1986; Lettenmaier & Gan 1990; Allen *et al.* 1991; Lettenmaier & Sheer 1991; Mimikou *et al.* 1991; Nash & Gleick 1991; Panagoulia 1992). Such scenarios have important implications for future water resources planning and management, the environment and the national economy.

Most hydrologic scenarios are based on the climatic predictions of numerical models of the general circulation of the atmosphere. General Circulation Models (GCMs) can produce long-term simulations of the energy and water fluxes in the atmosphere and land and ocean surfaces on a global computational grid of cells and a number of vertical layers. Predictions of changes in climatic variables such as precipitation and temperature are considered to be more reliable than those for runoff and soil moisture (Gleick 1989). The predictions are provided as spatial averages over areas of the order of 10^4 to 10^5 km² due to the limitations of present-day computers. Current GCMs perform reasonably well in simulating the present climate with respect to annual or seasonal averages at this spatial scale. However, the direct use of GCM outputs to drive hydrologic models is considered to be improper due to the coarse (relative to river basin scale) resolution

of the spatial grids used by GCMs and the simplified GCM representations of land surface processes, energy transfer within oceans, and subgrid-scale atmospheric processes such as convective storms. Moreover, GCM-based assessments of climate change are based on steady-state simulations of current climate and the climate associated with a doubling of current atmospheric concentrations of CO_2 , whereas in reality the concentration of CO_2 is increasing continuously. Despite these limitations, GCMs offer the most detailed quantitative information on potential large-scale climatic changes due to increasing atmospheric concentrations of trace gases.

Consequently, assessments of the impact of climate change on hydrologic systems frequently use doubled CO_2 scenarios consisting of a spectrum of uniform shifts to historical temperature series and scalings of historical precipitation series based on GCM trends. The size of the adjustment may vary from month to month to reflect seasonality in the assumed changes. Estimates of potential evapotranspiration for the changed climate scenarios are usually obtained by using simple scaling factors, sometimes varying seasonally, and by taking qualitative account of precipitation and temperature trends. The historical series and changed climate scenarios are used as input to mathematical models of hydrologic processes and the model outputs are evaluated to discern possible changes in soil moisture and water yield for a given catchment.

It is frequently argued that working with hypothetical scenarios suits the purpose of a sensitivity analysis of water resources and that results are not intended to be a prediction of changes. However, this approach suffers from three major limitations. First, it ignores any changes in the distribution and frequency of precipitation events and any changes in the nature and variability of temperature series. This may be regardless of whether such changes are indicated by

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GCM predictions. Second, the use of hypothetical scenarios based on an arbitrary number of temperature and precipitation perturbations and stationary wind and relative humidity series, say, is not realistic and may lack the internal consistency of GCM simulations of future climates. Third, concurrent historical climatic series are relatively short in length which may compromise the evaluation of the response of a hydrologic system to climate variability as well as climate change.

An alternative to the conventional approach is to use a stochastic model representing daily weather variations at a location. The parameters of such a model characterise the behaviour of the present day climate. Changed climate sequences can be produced by adjusting the model parameters in a manner consistent with GCM trends. The model is then used to generate long-term sequences of synthetic daily weather records which in turn are used to drive a hydrologic model (Wilks, 1992; Bates *et al.*, 1993; Charles *et al.*, 1993). Such an approach allows consideration of changes in the distribution and frequency of precipitation events and changes in the variability of other climatic variables. It also preserves the internal consistency of GCM simulations of future climates.

In this paper, an attempt is made to assess the impact of a doubling of current atmospheric concentrations of CO₂ on the North Para River at Penrice catchment in South Australia. Historical climatic and hydrologic series and results from a single GCM, a stochastic weather generator, and a conceptual water balance model have been used. Conclusions are drawn on possible changes in water yield as a result of climate change.

Methods

General circulation model

The GCM used in this study, *CSIRO9*, has been developed by the CSIRO Division of Atmospheric Research. The model operates with nine vertical levels in the atmosphere and a horizontal resolution of about 300 km \times 600 km. A computational time step of 30 minutes is used. The simulated climate data come from equilibrium (constant CO₂ concentration) runs for present day (control) and future (doubled CO₂) climates. A complete description of the model is given by McGregor *et al.* (1993).

Charles *et al.* (1993) reported distinct differences between the monthly rainfall patterns found in Australian meteorological station records and those in the *CSIRO9* control run. The differences were with respect to rainfall amount and its geographical distribution. Maximum daily grid cell rainfalls for *CSIRO9* control runs were also found to be between 1/4 and 1/5 of the maximum daily rainfalls recorded on mesoscale watersheds. Nevertheless, the comparison

of GCM rainfalls by Charles *et al.* revealed a general trend towards increasing rainfall amounts and changes in the rainfall occurrence process under doubled CO₂ conditions. The latter is consistent with the work of Gordon *et al.* (1992) who found marked changes in the magnitude and frequency of extreme rainfall events when comparing results from equilibrium experiments with the *CSIRO4* GCM.

Stochastic weather generator

The stochastic weather generator used in this study is based on the *WGEN* generator described by Richardson & Wright (1984). The daily climatic variables simulated by *WGEN* are precipitation occurrence and amount, maximum and minimum temperature, and global solar radiation (R_g).

Precipitation occurrence is described by a two-state (wet or dry day), first-order Markov chain. The transition probabilities for a given location are allowed to vary through an annual cycle by defining separate probabilities for each of the 12 calendar months:

$$p_{ij} = \Pr \{J_n = j \mid J_{n-1} = i\}$$

where p_{ij} = probability that a day in state i will be followed by a day in state j ($i, j = 0$ denotes a dry day; $i, j = 1$ denotes a wet day); and J_n = indicator variable denoting the presence or absence of precipitation on day n . The variation of precipitation amounts on wet days is characterised using either a gamma or mixed exponential distribution.

The temperature and solar radiation components are represented as

$$\mathbf{x}^*(t) = \mathbf{A}\mathbf{x}^*(t-1) + \mathbf{B}\mathbf{e}(t)$$

where $\mathbf{x} = (3 \times 1)$ vector of climatic variables; $\mathbf{e} = (3 \times 1)$ random forcing vector consisting of three independent standard normal variates; \mathbf{A} and $\mathbf{B} = (3 \times 3)$ matrices obtained from the lag-0 and lag-1 correlation matrices for the components of \mathbf{x} (Matalas, 1967); and the asterisk denotes standardisation:

$$x_k^*(t) = [x_k(t) - \mu_k(t)] / \sigma_k(t)$$

in which $k = 1, 2, 3$ and $j = 0, 1$; $\mu_k(t)$ = mean for climatic variable k and state j ; and $\sigma_k(t)$ = corresponding standard deviation. The annual cycles of μ_k and σ_k are modelled by single Fourier harmonics with fixed phase angles

Investigation of historical Australian daily maximum and minimum temperature series conditioned on wet and dry days has shown that the use of a single harmonic to describe annual cycles of means and standard deviations is often unjustified. Higher harmonics are present in the mean series and the standard deviation series are more realistically represented by fixed monthly values. (see also McCuskill 1992). Thus a mean temperature series (\bar{T}) may be written as

$$\bar{T}_{kj}(t) = \mu_{kj} + \sum_{r=1}^m R_{kr} \cos [2\pi r (t + \phi) / 365] + \epsilon_r$$

where $k = 1, 2$; $j = 0, 1$; t = Julian date, μ = constant; $m \leq 3$; R_r = amplitude of the r th harmonic; $\pi = 3.14$ in this case; ϕ = phase angle; and ϵ_r = r th residual.

Similarly, investigation of Australian solar radiation series has indicated that the fitting of single harmonics, the use of a fixed phase angle and the use of the generation scheme defined above is an inadequate approach (see Bates *et al.* 1993). Our approach involves the calculation of the upper envelope for clear day conditions, R_{0+} . (A documented FORTRAN-77 computer program for calculating the upper envelope can be obtained from the authors). This theoretical maximum is based on geographical location and average clear day atmospheric conditions. For each calendar month, a generalised beta distribution is fitted to the daily residuals (the difference between the theoretical maximum and recorded data) for wet and dry days.

Climate sequences for doubled CO₂ conditions

Wilks (1992) presented a method for the adaption of stochastic daily weather models fitted to current climatic series to the generation of synthetic series for future climates. The adjustments to the model parameters were made in a manner consistent with the changes in monthly statistics derived from comparisons of GCM runs for control and doubled CO₂ conditions. This approach was based on the notion that GCM results are often available in terms of monthly rather than daily values or even monthly means and variances. The CSIRO GCM runs provide daily values for 30 climatic variables for 30 year periods. The variables include: precipitation; humidity at level 1; maximum and minimum screen temperature; temperature at level 1; and net solar radiation at ground level (R_{0+}). Consequently, our method for making parameter adjustments to stochastic daily weather models uses this information.

Let P = monthly precipitation for a month comprised of N days. The mean of P and its variance are defined by (Wilks 1992)

$$\mu(P) = N\pi\alpha\beta$$

$$\sigma^2(P) \approx N\pi\alpha\beta^2 [1 + \alpha(1 - \pi)(1+d)/(1-d)]$$

where π = unconditional probability of a wet day [$\pi = p_{01}/(1 + p_{01} - p_{11})$]; α, β = shape and scale parameters of the gamma distribution; and $d = p_{11} - p_{01}$ is a measure of persistence. For simulating doubled CO₂ conditions, we construct the ratios (Wilks 1992):

$$\frac{\mu(P')}{\mu(P)} = \frac{\pi'\alpha'\beta'}{\pi\alpha\beta}$$

$$\frac{\sigma^2(P')}{\sigma^2(P)} = \frac{\pi'\alpha'\beta'^2 [1 + \alpha'(1 - \pi')(1 + d')/(1 - d')]}{\pi\alpha\beta^2 [1 + \alpha(1 - \pi)(1 + d)/(1 - d)]}$$

where the prime denotes doubled CO₂ conditions. The solution of the above equations requires two additional constraints. For catchments in the arid and semi-arid regions of Australia where $\pi < 0.5$, we set $\pi' = \pi\pi_2/\pi_1$ and $d' = dd_2/d_1$ in which the subscripts 1 and 2 denote GCM values for a nearby GCM grid cell for control and doubled CO₂ conditions, respectively.

For mean doubled CO₂ daily maximum and minimum temperatures, we assume:

$$\bar{T}'_{kj}(t) = \bar{T}_{kj}(t) + \bar{T}'_k(t) - \bar{T}^1_k(t)$$

where the prime denotes doubled CO₂ conditions; \bar{T} = harmonics fitted to the observed mean series; and \bar{T}^1, \bar{T}^2 = harmonics fitted to screen temperatures from the control and doubled CO₂ GCM runs, respectively. Standard deviations are assumed to be unchanged.

Clear day solar radiation is affected by precipitable water content and CO₂ concentration. Here we derive daily level 1 vapour pressures using the temperatures and relative humidity at level 1 and hence upper envelopes for the control and doubled CO₂ GCM runs. The GCM solar radiation is $R_0 = R_{0+} / (1 - a)$ where a is the albedo assigned to the GCM grid cell. Generalised beta distributions are fitted to the corresponding residuals ($R_{0+} - R_0$) for each calendar month and rainfall state. Parameter estimates for doubled CO₂ residual distributions are obtained by the method of moments. Here the historical residual means and variances for each month are scaled by the ratios of the corresponding doubled CO₂ and control means and variances, respectively. The upper envelope for doubled CO₂ conditions is obtained by scaling historical daily vapour pressures by the ratio of derived doubled CO₂ and control GCM vapour pressures.

Water balance model

A modified version of Boughton's (1984) *SFB* model was used for the study (Fig. 1). The model uses daily rainfall and potential evapotranspiration data as input to estimate monthly streamflow. The original model has three parameters requiring calibration: the surface storage capacity (S), the daily infiltration capacity (F) controlling the movement of water from the surface store to lower store; and the baseflow factor (B) determining the portion of the daily depletion of water in the lower store that appears as baseflow ($0 \leq B \leq 1$). The four remaining parameters are fixed: the fraction of the surface storage capacity that does not drain to the lower store ($NDC = 0.5$); the maximum limiting rate of evapotranspiration ($E_{max} = 8.9 \text{ mm d}^{-1}$); the lower store depletion factor ($DPF = 0.005$); and a baseflow threshold for the lower store ($SDR_{max} = 25 \text{ mm}$) defining the depth of water in the lower store at which baseflow will cease.

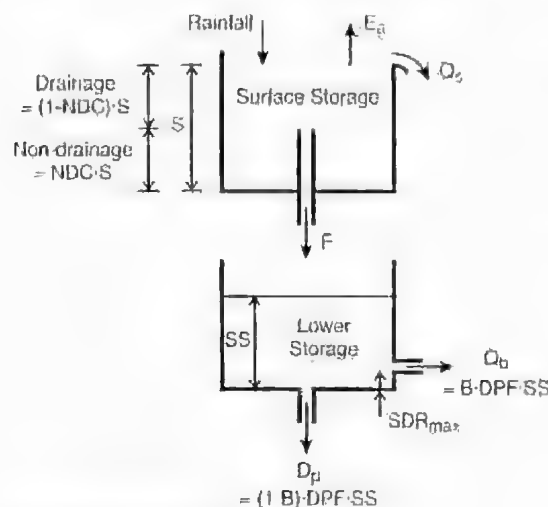


Fig. 1. Structure of the *SFB* model.

The model operations may be summarised as follows. Rainfall begins to fill the surface store and any water in excess of the non-drainage component of that store infiltrates into the lower store at a maximum daily rate of $F \text{ mm d}^{-1}$. Surface runoff (Q_s) occurs when the drainage component of the surface store is full and may be written as

$$Q_s = P - F \tanh(P/F)$$

where P = rainfall excess remaining after the surface store is filled. The surface store contents are depleted by evapotranspiration which occurs at the potential rate (E_{pot}) when the non-drainage component is full.

Otherwise, the actual evapotranspiration rate (E_a) is given by

$$E_a = \min \{E_{max}S / (NDC.S); E_{pot}\}$$

where s = depth of water in the non-drainage component of the surface store. The lower store is depleted by deep percolation (D_p) and baseflow (Q_b) which are defined by

$$D_p = (1-B).DPF.SS$$

$$Q_b = B.DPF.(SS-SDR_{max})$$

where SS = depth of water in the lower store.

In this study, estimates of daily potential evapotranspiration in mm d^{-1} were obtained using the Priestley-Taylor equation (Priestley & Taylor 1972):

$$L E_{pot} = \alpha R_n \Delta / (\Delta + \gamma)$$

where L = latent heat of vaporisation in MJ kg^{-1} , $\alpha = 1.3$ in this study, Δ = slope of the vapour pressure curve in $\text{kPa}^\circ\text{C}^{-1}$, R_n = net radiation in $\text{MJ m}^{-2} \text{d}^{-1}$, and γ = psychrometric constant in $\text{kPa}^\circ\text{C}^{-1}$.

Although the *SFB* model parameters have some physical basis, they cannot be readily determined by physical measurement. Thus parameter estimates must be obtained by fitting computed to observed monthly streamflow hydrographs. Formal optimisation techniques can be used to facilitate the estimation process. These techniques use a subjectively chosen criterion (the 'objective function') to quantify discrepancies between the computed and observed hydrographs for a given set of parameter values. The estimates of the model parameters are those parameter values which result in the minimum possible value of the objective function. The accuracy of these estimates affects the accuracy of streamflow predictions.

In this study, the estimates for the *SFB* model parameters were obtained using a simulated annealing algorithm (Kirkpatrick *et al.* 1983; Press *et al.* 1992). Simulated annealing is a stochastic, multivariate optimisation technique which seeks the global or near global minimum of a user-defined objective function without getting trapped in a local minimum. The function need not be smooth or even continuous in its domain. The method can be considered as a biased random walk that samples the full parameter space and provides a solution that is independent of the starting

point. It can accept a 'move' that increases the value of the objective function as a part of a full series of moves for which the general trend is to decrease the function value. Details of the algorithm used will be published elsewhere.

The objective function used in this study may be written as

$$\min_{\theta} \sum_{i=1}^n z_i^2$$

where the model parameters vector $\theta = (S, F, B, NDC, E_{max}, DPF, SDR_{max})'$ in which the prime denotes the transpose of a vector; n = number of months in the observed streamflow hydrograph record; k = number of months in the 'warm-up' period which is excluded from the calculation of the objective function value; and the disturbance z_i is defined by

$$z_i = (Q_i + \lambda_1) - (\bar{Q}_i + \lambda_2) \quad / \lambda_1, \quad \lambda_1 \neq 0, \lambda_2 \geq 0$$

in which Q = observed streamflow; \bar{Q} = computed streamflow ($\bar{Q} = Q_b + Q_e$); and λ_1, λ_2 = transformation constants which can be estimated by trial and error (Bates & Watts 1988). Generally, the best fits are obtained with $\lambda_1 < 1$ and $\lambda_2 \approx 0$.

Case Study

Description of catchment and data

The above methodology was applied in the North Para River at Penrice catchment in South Australia. The catchment comprises an area of 118 km² and is located within the Gawler River basin some 50 km north east of Adelaide. It rises from 300 m to 500 m AHD and has duplex soils and a mixed ground cover¹. Land use includes horticulture, viticulture, grazing, and arable farming.

Daily streamflow at the Penrice gauging station (34° 28'S, 139° 4'E) and daily rainfalls recorded at Angaston Post Office (34° 30'S, 139° 3'E) and Keyneton (34° 33'S, 139° 8'E) for the period January 1978 to December 1989 were used in the study. Over this period, the mean annual runoff was 6,200 MJ (50 mm) and the mean annual rainfall (65% of which falls in the period May to September) was 550 mm. The average daily maximum winter and summer temperatures were 13°C and 29°C, respectively (Chiew & McMahon 1993¹).

Estimates of daily potential evapotranspiration were obtained using the guidelines described by Smith (1991), clear day radiation and day length estimates, and temperature and sunshine hours data from the Nuriootpa Viticultural climate station (34° 29'S, 139° 0'E) which is located some 10 km from the catchment centroid.

Model calibration

Preliminary investigations revealed that the performance of the 3-parameter *SFB* model was inadequate. However, satisfactory model fits were obtained by setting $\lambda_1 = 0.6$, $E_{max} = 8.9$ mm d⁻¹, $NDC = 0.5$, $SDR_{max} = 0$ mm, and allowing the parameters S , F , B , and DPF to vary during calibration runs. The final parameter estimates obtained were: $S = 165$ mm; $F = 0.9$ mm d⁻¹; $B = 0.414$; and $DPF = 0.12$. The B and DPF estimates indicate that there is a significant loss of water from the catchment to the regional groundwater.

An important assumption in this study is that the *SFB* model is able to simulate runoff from the North Para catchment under climatic conditions that are different to those for which the model has been calibrated. For example, the effect of possible changes in plant transpiration rates and vegetative cover due to CO₂ doubling on the model parameters is ignored. This was considered to be a reasonable assumption given the current level of uncertainty regarding the nature and magnitude of these changes.

Results

To simplify the analysis of the results, the behaviours of three variables under control (1 × CO₂) and doubled CO₂ (2 × CO₂) conditions were examined: (1) monthly rainfall; (2) monthly evapotranspiration; and (3) monthly total runoff. Synthetic climatic sequences of 1,000 years duration were generated for control and doubled CO₂ conditions and used to drive the *SFB* model. Exploratory analyses of the data revealed that the variable distributions were highly skewed. Thus the median rather than the mean was adopted as the measure of central tendency.

Fig. 2 compares the distributions of simulated monthly rainfall for control and doubled CO₂ conditions. Three features are worthy of note under doubled CO₂ conditions: (1) there is an increase in minimum monthly rainfall for the period from June to August and a decrease for the months of May, September and October; (2) median rainfalls for the period from March to November are greater than or equal to those for present day conditions; and (3) there are marked increases in extreme (high) rainfalls for the month of January and the period from August to October.

Fig. 3 compares the distributions of modelled monthly evapotranspiration for control and doubled

¹ CHIEW, F. H. S. & MCMAHON, T. A. (1993) Complete set of daily rainfall, potential evapotranspiration and streamflow data for 28 unregulated Australian catchments. Centre for Environmental Applied Hydrology, University of Melbourne, 53 pp. (unpubl.)

TABLE 1. Seasonality and distribution of monthly runoff for control and doubled CO₂ conditions.

Percentile	Monthly Runoff (mm)*											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Minimum	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
10th	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.7 (1.4)	1.0 (0.4)	0 (0)	0 (0)	0 (0)
30th	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.3 (1.5)	7.3 (7.2)	5.0 (4.3)	0.3 (0.3)	0 (0)	0 (0)
50th	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.0 (5.0)	10.8 (10.6)	8.7 (8.1)	1.4 (1.7)	0 (0)	0 (0)
70th	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (1.4)	8.7 (8.8)	11.7 (11.7)	11.0 (11.0)	4.2 (4.3)	0.1 (0.1)	0 (0)
90th	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5.8 (6.1)	11.6 (11.6)	17.4 (16.0)	11.4 (13.9)	8.5 (8.5)	0.5 (0.6)	0 (0)
99th	0 (0)	0 (0)	0 (0)	0 (0.1)	3.5 (4.7)	10.9 (10.8)	36.7 (44.7)	61.5 (65.1)	40.4 (59.5)	11.8 (16.9)	3.9 (3.7)	0.1 (0.2)
Maximum	0 (2.0)	0 (2.5)	0.6 (0.2)	4.9 (2.7)	11.0 (10.5)	41.2 (30.1)	69.5 (96.6)	99.2 (145)	53.2 (103)	51.9 (82.3)	6.8 (7.6)	0.4 (1.0)

* Values in parentheses are for doubled CO₂ conditions.

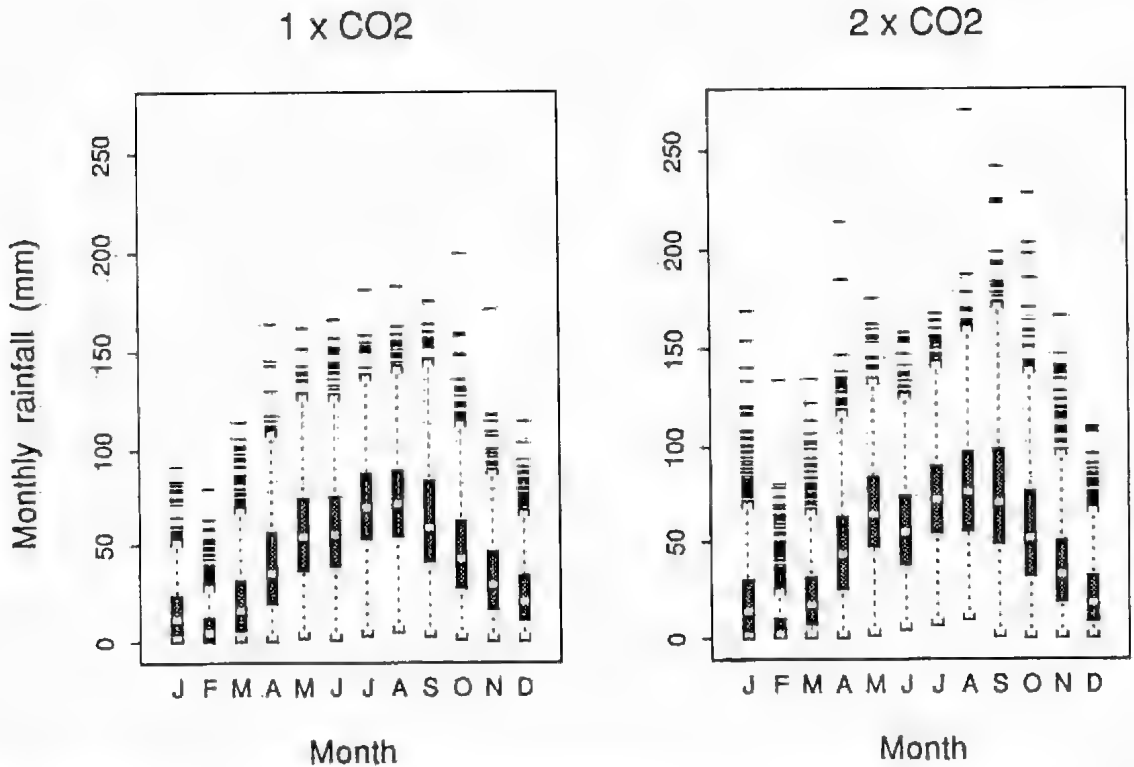


Fig. 2. Box plots of modelled monthly rainfall for control ($1 \times \text{CO}_2$) and doubled CO_2 ($2 \times \text{CO}_2$) conditions. [Edges of boxes mark upper and lower quartiles, and horizontal blank line within each box depicts the median. Distance between the quartiles is the interquartile range (IQR). End points of whiskers attached to boxes denote either data extremes (no adjacent horizontal lines) or adjacent values defined by upper quartile plus $1.5 \times \text{IQR}$ and lower quartile minus $1.5 \times \text{IQR}$. Horizontal lines mark data points that lie beyond adjacent values.]

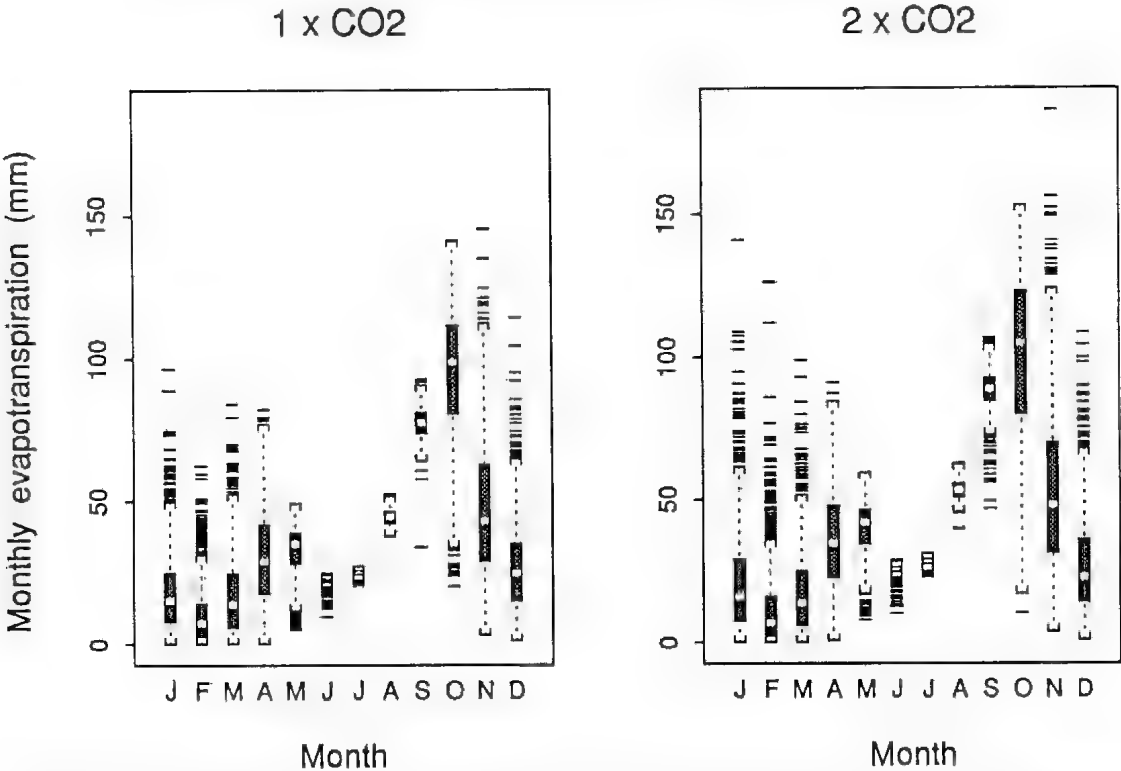


Fig. 3. Box plots of modelled monthly evapotranspiration for control (1 × CO₂) and doubled CO₂ (2 × CO₂) conditions.

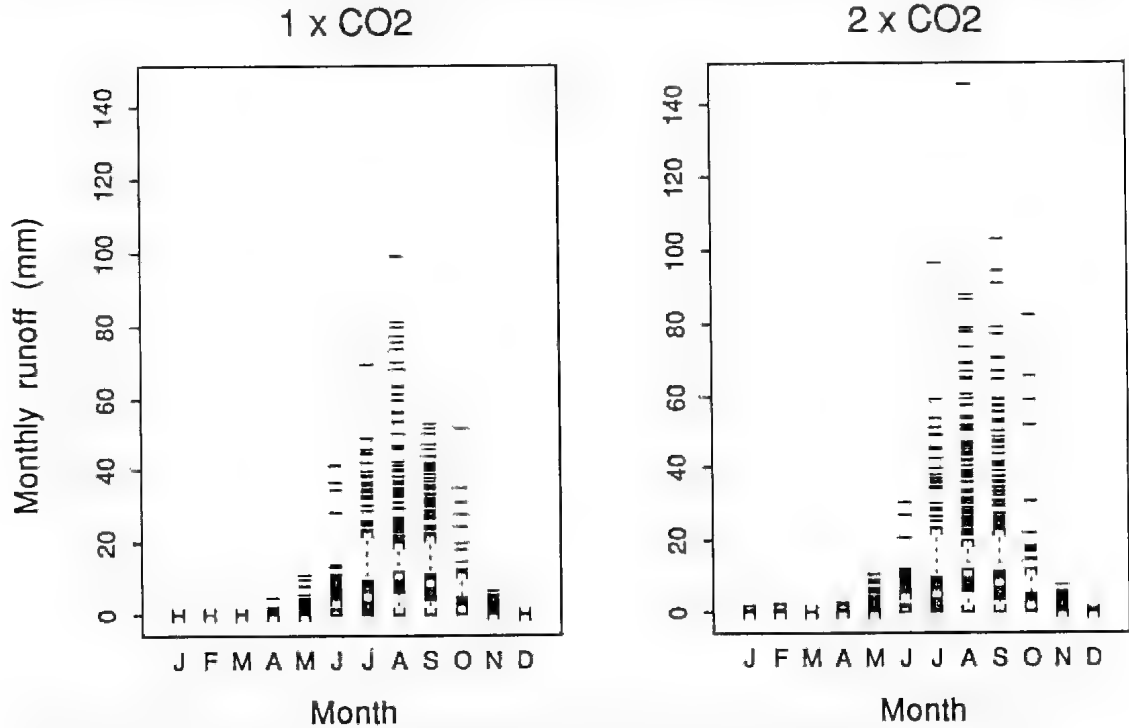


Fig. 4. Box plots of modelled monthly runoff for control (1 × CO₂) and doubled CO₂ (2 × CO₂) conditions.

CO₂ conditions. There appears to be a general increase in evapotranspiration for the period from March to November under doubled CO₂ conditions. Furthermore, a review of evapotranspiration values greater than the 75th percentile point revealed an increase in high evapotranspiration values over the entire year. The size of the increase is quite large for the months of January, February and November.

Table 1 lists various percentile points for simulated monthly runoff for control and doubled CO₂ conditions. The distributions of the runoff data are also illustrated in Fig. 4. Overall, there is little evidence of changes in the median and upper and lower quartiles of monthly runoff. However, it is evident that the extremes (high runoff values) for the doubled CO₂ climate are greater than those for present day conditions for the period from July to October. There are also indications of reductions in the 10th, 30th and 50th percentile points for September.

Fig. 5 shows an empirical quantile-quantile plot of the annual maxima of monthly runoff. The annual maxima for both conditions are very similar for maxima below their medians (about 11 mm). Above the medians, the maxima are higher for the doubled CO₂ climate than for the present day and the difference between the series appears to grow with increasing percentile rank. Thus there is a suggestion of an increase in flood risk. A review of the maxima revealed that the extreme events were due to the marked increases in extreme rainfalls and modest increases in evapotranspiration for August and September under doubled CO₂ conditions.

Conclusions

The most prominent effect of doubled atmospheric concentrations of carbon dioxide on the water yield of the North Para River catchment, South Australia, is a sizeable increase in the annual maxima of monthly runoff. This may indicate an increase in flood risk. However, there appears to be little impact on the seasonality and magnitude of the median and upper and lower quartiles of monthly runoff.

The above results highlight the benefits of using stochastic weather generators in assessments of the impact of climate change on hydrologic systems. The estimation of extreme hydrological events based on original and perturbed historical records are not reliable when the return periods of these events are of the order of the original record length. An impasse arises when the return periods of interest are greater than the period of record. Thus the length of the historical record limits what can be said about the changes in the tails of the distributions of hydrologic variables that may be caused by CO₂ doubling. In contrast, our approach is capable of producing climatic and hydrologic series of arbitrary length. This enables a more detailed investigation of changes in interannual variability.

The results presented herein were obtained using one GCM (CSIRO9), a stochastic weather generator and a water balance model (SFB). Thus the quality of the results rely heavily on the accuracy and relevance of these models and the implicit assumption that the long-term changes in vegetation that would be associated with CO₂ doubling represent a second-order effect. Nevertheless, it can be argued that the present generation of GCMs are fundamentally similar and that they differ principally with respect to their parameterisation of certain processes such as cloud formation and rainfall. Thus the use of one rather than a suite of GCMs should not seriously compromise the results of this study.

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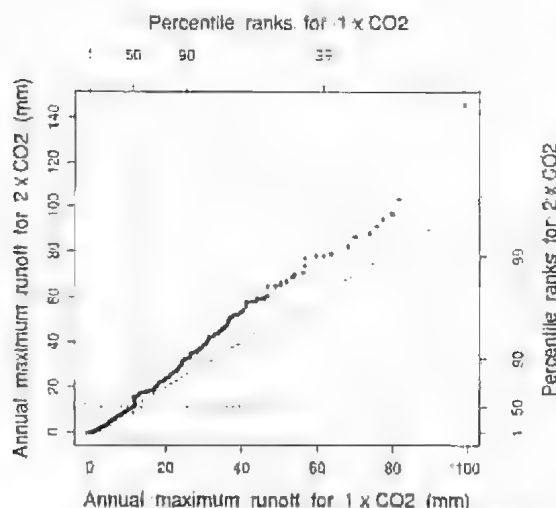


Fig. 5. Empirical quantile-quantile plot of annual maxima of monthly runoff for control (1 \times CO₂) and doubled CO₂ (2 \times CO₂) conditions.

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IMPLICATIONS OF CLIMATE CHANGE FOR THE SOUTH AUSTRALIAN COASTLINE

BY NICK HARVEY & TONY BELPERIO†*

Summary

Harvey, N. & Belperio, T. (1993) Implications of climate change for the South Australian coastline. *Trans. R. Soc. S. Aust.* (1994) 118(1), 45-52, 31 May, 1994.

Recent attention has been focused on the effects of climatic change on sea level and the effects of a rising sea level on coastal environments. However, the variation in physical and geological processes which are responsible for sea level change is often overlooked or underestimated. This paper presents recent geological and tide gauge data from South Australia to demonstrate that neotectonic and anthropogenic influences have resulted in a general overestimation of the current rate of sea level rise, apart from two sites where the reverse is true. The paper concludes that all tide gauge sites must be corrected for vertical crustal movements before any conclusions are drawn regarding local or global sea level change. The implications of this for South Australian coasts are that adjustments to sea level trends should be made before any vulnerability assessments are conducted.

Key Words: sea level change, coastal environments, climate change, vertical crustal movements, South Australia.

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Introduction

The recent Greenhouse debate has focused attention on the effects of climatic change on sea level (Warrick *et al.* 1993) and also the effects of a rising sea level on coastal environments (Bird 1993; Tooley & Jelgersma 1992). In addition, the work of the Intergovernmental Panel on Climate Change (IPCC) has produced scientific assessments of climatic change (Houghton *et al.* 1991; Houghton *et al.* 1992), together with the IPCC Common Methodology for assessing the vulnerability of coastal areas to sea level rise (IPCC 1991). However, there has been some criticism of the applicability of this IPCC Common Methodology to the Australian region (Kay *et al.* 1992; Woodroffe & McLean 1993).

Before discussing the implications of this recent research for the South Australian coast, it is important to note that there is a great variation in physical and geological processes which are responsible for sea level change. These variations, which have been categorised by Pugh (1993) in terms of their spatial and temporal influence, can vary considerably from short term wind waves with periods of about 10 seconds and an extent of tens of metres, up to global changes in sea level related to sea floor spreading with time periods of hundreds of millions of years. In addition, the process of redistribution of mass over the earth resulting from deglaciation, addition of meltwater to the oceans and transgression and regression over the continental shelves, itself results in a variety of isostatic responses of the crust to the changing loads. The resultant lack of uniformity in global sea level change is often overlooked or underestimated.

Perhaps the most studied geological period in terms of sea level change is the Quaternary (Williams *et al.* 1993) where the effect of climatic change has resulted in numerous fluctuations of sea level in response to the waxing and waning of continental ice sheets. Consequently there has been alternate flooding and exposure of continental margins together with periods of erosion and sedimentation.

The most recent time when climatic conditions and sea level were similar to the present was during the last interglacial period at around 125,000 years before present (BP) when sea level in the Australian region was between 2 and 8 m higher than today (Chappell 1987). Since then, sea level fluctuations have always been lower than present with evidence from the Australian region of a low sea level of between 130 and 165 m lower (Chappell 1987) at 18,000 years BP, after which it rose at a rate of between 6 and 12 mm yr⁻¹ prior to reaching its present level between 6000 and 7000 years BP.

It is in the record of the last 6000 years that scientists have focused attention on finding evidence for any long term trends in sea level either by direct sea level indicators in the geological record or by analogous paleoclimatic change evidence. Careful field studies from many coastal localities have supported geophysical models which indicate that subtle differences in sea level behaviour are the norm even for the South Australian coast, long regarded as stable and uniform (Lambeck & Nakada 1990).

There has also been direct measurement of sea level and detailed analysis of recent tide gauge records to extrapolate relative trends (Gornitz 1993; Pirazzoli 1991). As noted by Bird (1993) there are numerous factors affecting relative sea level change. Apart from eustatic sea level change there is the tectonic response of the land and the isostatic response of the continental margins relating to changing volumes of ice, water or

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sediment. In addition, human activities such as groundwater or hydrocarbon extraction, land reclamation, artificial coastal structures, dredging and pumping of sediment can affect local sea level change. Pirazzoli (1989) suggested that local secular tide gauge data are dominated by neotectonic and anthropogenic effects, resulting in an over-estimation of global sea level rise by 2 to 3 times when these factors are ignored.

South Australian policy of coast protection and new development

The current South Australian policy on coast protection and new coastal development was prepared by the Coast Protection Board and endorsed by the South Australian Government in May 1991. The policy, which is described in detail elsewhere (Coast Protection Board 1992), relies in part on local records of coastal erosion, flooding and sea level rise but more importantly has incorporated the IPCC estimates of greenhouse induced eustatic sea level rise. These estimates predict a sea level rise to the year 2100 of approximately 0.65 m (range 0.33 m to 1.10 m) for a "business as usual" scenario (Houghton *et al.* 1991). Given these estimates the Coast Protection Board used the "precautionary principle" in preparing its policy. The precautionary principle which was adopted by all Australian governments states that "where there are threats of serious or irreversible environmental damage, lack of full scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation" (Intergovernmental Agreement on the Environment 1992, para 3.5.1).

In accordance with this principle the Coast Protection Board has adopted the policy that any new coastal development should be capable of being reasonably protected from a 1 m sea level rise by the year 2100. The policy establishes the 100 year average return interval (ARI) water level as a standard for coastal development in South Australia. It recommends that site and building levels should be determined by adding 0.3 m to the 100 year ARI water level and (where appropriate) making an adjustment for localised subsidence or uplift. Floor levels of buildings should be an additional 0.25 m above this level, and buildings should not be approved unless they are capable of being protected or raised to withstand a further 0.7 m of sea level rise (e.g. by means of a bund wall). In the case of flood protected sites, the calculation of the 100 year ARI design flood level must incorporate the extreme tide (plus surge) and stormwater events, together with wave effects within the development.

The policy also makes a general recommendation for an erosion setback distance. This is to be based upon 100 years of erosion at a site, allowing for local coastal processes and a sea level rise of 0.3 m to the year 2050, and taking account of storm erosion from

a series of severe storms. For major coastal development it is suggested that calculations are based upon 200 years of erosion.

The policy is less specific about the protection of existing property although it reaffirms an earlier Government policy not to protect private property. Although part of the Coast Protection Board's duties are to protect the coast, most coast protection works are carried by local councils. According to the 1991 policy statement, the Coast Protection Board provides councils with grants of up to 80% of the cost of approved coast protection works and up to the same amount for storm damage repairs. The issue of cost sharing between State and local government is currently an issue of debate but the underlying question for any protection works is essentially a decision whether to protect or relocate. This is complicated by the level of public or private involvement and the relative responsibilities of State and local government. For this reason the Coast Protection Board and local government determine these issues on a case by case situation.

Global sea level rise estimates

A major problem in identifying the current rate of eustatic sea level change from tide gauge data is the influence of neotectonic, isostatic and anthropogenic effects, compounded by a geographical bias in the distribution of reliable tide gauge data (Warrick 1993; Gornitz 1993; Aubrey & Emery 1993; Woodworth 1993). These problems create uncertainty in extrapolating the eustatic component of sea level change and has led authors such as Aubrey & Emery (1993) to expressed caution in attempting to extrapolate actual sea level changes from the data. They suggest that the apparent post 1930 accelerated sea level rise may be related to factors other than human induced factors such as a delayed response to climatic warming following the Little Ice Age, oceanographic factors, or perhaps may not even be statistically significant.

Other authors such as Gornitz (1993) suggest that after extraction of long-term trends and data averaging, that it is possible to obtain a true picture of sea level rise. Gornitz presents evidence based on 16 tide gauge data studies to suggest that estimates of global sea level rise over the last 100 years has been between 0.5 and 3 mm yr⁻¹, with most estimates in the range of 1 to 2 mm yr⁻¹ (Gornitz 1993).

In addition to studies attempting to identify eustatic sea level changes based on analysis of tide gauge data, there are also a number of studies on sea level rise projections related to climate change. The key study has been the IPCC sea level rise predictions with a best estimate of a 0.65 m rise to the year 2100 (Houghton *et al.* 1990) upon which the South Australian coastal policy has been based. The IPCC

report provided a significant downwards revision of earlier sea level rise predictions but more recent calculations have continued to produce similar best estimate figures either by more qualitative expert analysis (0.61 m by the year 2087, Woodworth 1993), or by detailed re-calculation (0.46 m by the year 2100, Wigley & Raper 1993).

The South Australian coast: Secular sea level rise

Records of sea level in Australia, from the period 1897 to present, have been monitored and analysed by the National Tidal Facility (NTF) at Flinders University in South Australia. As for the global situation, there is significant spatial inhomogeneity in the secular sea level trends resulting from the myriad

of factors affecting relative sea level behaviour at each tide gauge site. Although there is a variation in the quality of tidal records available, the NTF analysis of tidal data from gauges with an acceptable datum stability indicate an Australian average of $1.51 \pm 0.18 \text{ mm yr}^{-1}$ at the 95% confidence level (Mitchell 1991). This figure is in agreement with global analyses of $1.0\text{--}2.0 \text{ mm yr}^{-1}$ (Gornitz 1993), notwithstanding the caution expressed about the validity of these figures (Aubrey & Emery 1993).

South Australian sea level trends based on tide gauge data (see Fig. 1 for location of tide gauges) have been presented by Mitchell (1991), although there are significant tidal records such as Port Augusta, which have yet to be analysed by the NTF (Table 1).

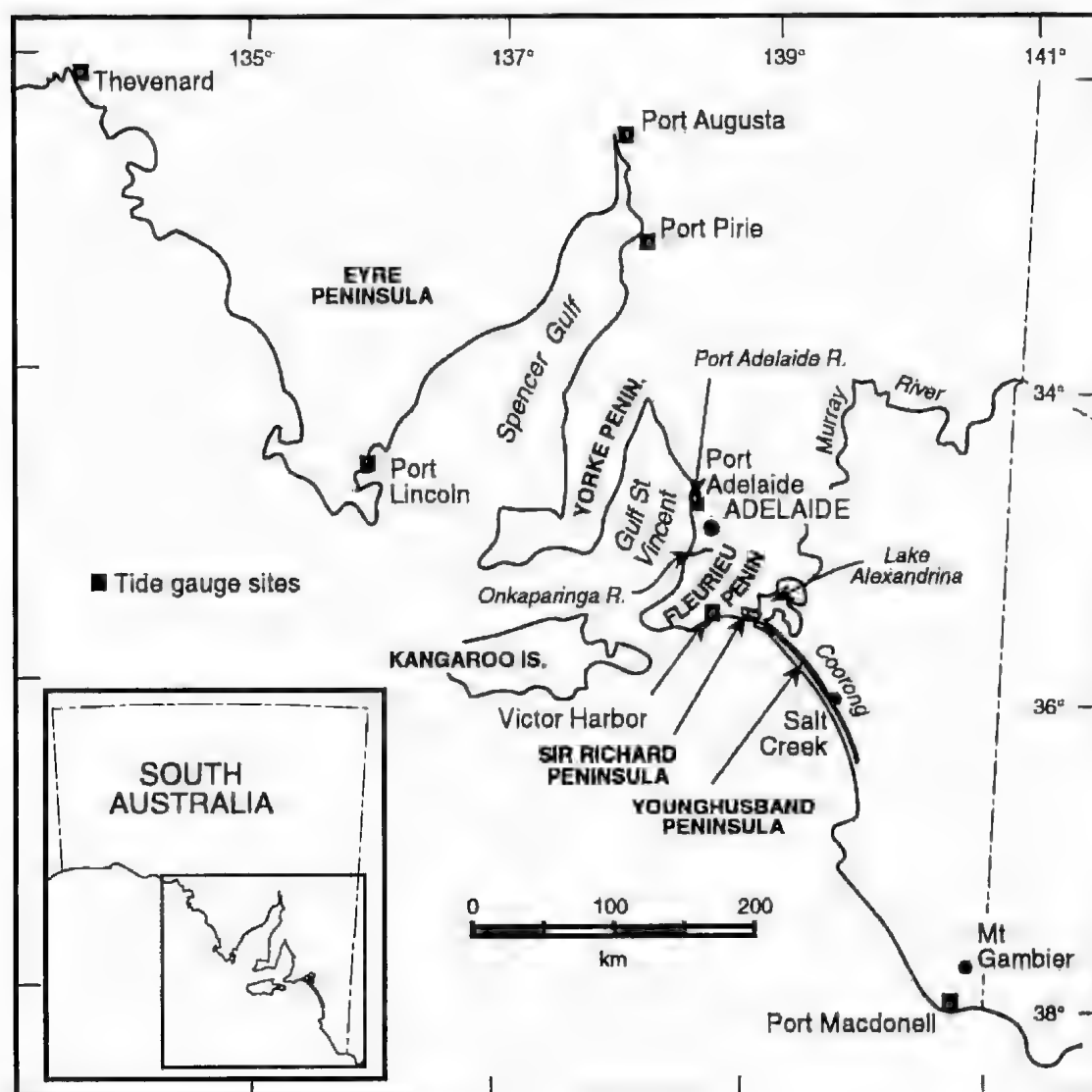


Fig. 1. Location of tide gauges in South Australia.

South Australia — Neotectonic contribution to sea level change

Australia is frequently, and incorrectly, quoted as a stable continent from which absolute sea levels can be measured. Neotectonic movements caused by structural geoidal and isostatic processes, together with factors such as sediment compaction, affect Australia at various spatial and temporal scales. This complexity of underlying factors that control relative sea level change has been demonstrated by the reconstruction of palaeo-sea level histories from numerous sites around Australia and South Australia.

The sea reached its present level around the South Australian coast between 7000 and 6000 yr BP. South Australia is in the "far field" in its response to global deglaciation, and is affected by subtle, ongoing isostatic adjustment of shelf and coast. This is manifested as an apparent highstand of the 6000 yr BP shoreline (Fig. 2), the height of which varies systematically and predictably around the coast. In particular, the height

of the highstand increases up the two gulfs with increasing distance from the continental margin. Sea level change over the past few thousand years is dominated by this regression, which increases in magnitude from 1 m or less along Eyre Peninsula to 3.0 m at the head of Gulf St Vincent and 4.5 m in Upper Spencer Gulf. Isostatic adjustments thus vary from 0.1 mm yr⁻¹ to 0.8 mm yr⁻¹ averaged over these time scales. This has caused slow but obvious coastal regression, particularly at the heads of both gulfs.

Superimposed on this geographically variable Holocene isostatic warping are longer term tectonic movements. Tectonic effects are most noticeable along the South East coastal plain, between Lake Alexandrina and Mt Gambier, where Quaternary volcanism has resulted in ongoing uplift and tilting of the coastal plain. The scale and variability of this upwarp can be illustrated by the changing elevation of the last interglacial shoreline (Fig. 3). This 125,000 year old shoreline rises progressively southwards, from 3 m above present sea level at Salt Creek, to in excess of 18 m near Port Macdonnell. Uplift rates in the Port Macdonnell region are a minimum of 0.2 mm yr⁻¹ if averaged out over this entire time period.

Another under-rated effect associated with cities is sediment compaction and land subsidence associated with coastal reclamation and withdrawal of underground fluids (Bird 1993). Such effects are local, but are sufficiently frequently associated with harbours and tide gauge sites as to seriously question the validity of global averages obtained from their secular trends (Davis 1987; Pirazzoli 1989).

The local record from Port Adelaide clearly illustrates these effects and the inherent danger of using tide gauge data without adequate neotectonic correction (Belperio 1989, 1993). Data from tide gauges, mangrove migration patterns and from dated subsurface strata all indicate a contemporary relative rise in sea level within the Port Adelaide estuary. The geographic restriction of these effects to the Port Adelaide region, together with preliminary geodetic evidence, indicate that the apparent rise in sea level is a local phenomenon, resulting chiefly from subsidence of the land. Belperio (1993) concluded that up to 1.0 m of surficial compaction and land lowering had occurred in association with wetland reclamation, acid sulphate soil development, increasing urban and industrial development and groundwater withdrawal. Highly variable rates of land subsidence, between 1.8 and 10 mm yr⁻¹, were estimated to be occurring over different parts of this region. More significantly, some three quarters of the secular rise of sea level indicated by the Port Adelaide and Outer Harbor tide gauge data could be attributed to land subsidence over the last 50 years at this location.

Corrections to tide gauge derived sea level trend data should be made for these various neotectonic

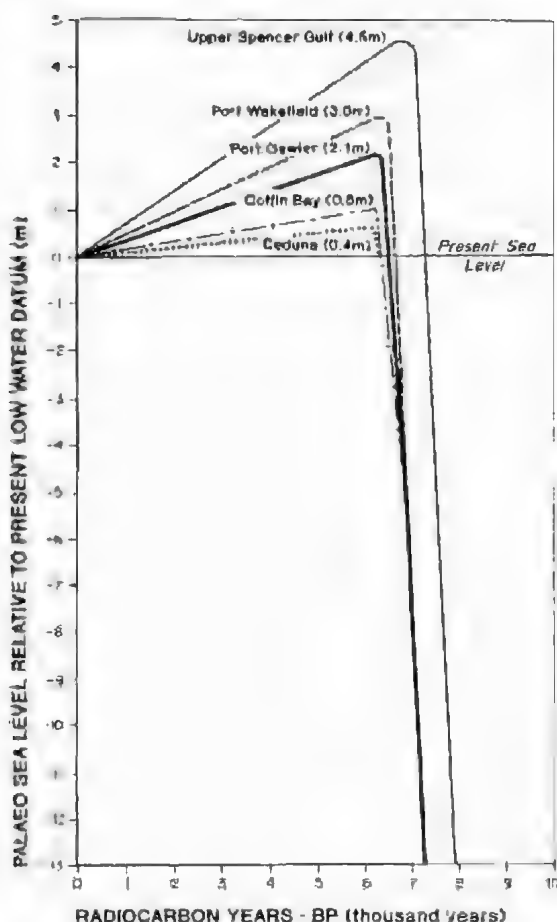


Fig. 2. Palaeo sea levels relative to present sea levels at various sites in South Australia

contributions. Preliminary corrections have been made for South Australian tide gauge sites incorporating known neotectonic variations (Table 1). The tide gauge data from Port Adelaide and Outer Harbor have been used in global and Australian sea level rise averages without adequate local neotectonic correction. Many of the world's tide gauges are similarly biased by land subsidence effects, indicating the importance of making such local neotectonic corrections to all tide gauge data before inferring local or global sea level changes.

TABLE 1. Sea level trends calculated from South Australian tide gauge data.

	years of record	trend ¹ mm yr ⁻¹	preliminary adjusted trend ² mm yr ⁻¹
Port Adelaide (Outer Hb)	48.2	2.82	0.6
Port Adelaide (Inner Hb)	35.1	2.28	0.5
Port Lincoln	25.4	0.90	0.7
Port Macdonnell	21.7	0.49	0.6
Port Pirie	51 ²	-0.20 ²	0.3
Thevenard	24	1.14	1.0
Victor Harbor	23.8	1.17	1.1

*Source: (Mitchell 1991, p. 355) except ² Mitchell 1993, pers. comm.) ³ this paper.

Vulnerability of the South Australian coast to sea level rise

A number of papers presented at the Australian "Greenhouse 87 Conference" discussed the general coastal impacts of a greenhouse sea level rise around the Australian coast (see Pearman 1985). However, very little work has been conducted on the vulnerability of the South Australian coast to current erosion

processes, or on the effects of an accelerated sea level rise. Harvey (1993) provides data on the sensitivity of selected South Australian coastal environments to development. Fotheringham & Caton (1989) give a broad overview of potential impacts of a greenhouse sea level rise on the South Australian coast, and Wynne (1989) examines implications of a sea level rise for coastal erosion and flooding.

The South Australian coastline is approximately 4000 km long including a variety of coastal landforms, including cliffed coasts, rocky outcrops, mangroves, mudflats, extensive sandy beaches, coastal dunes, and a number of off-shore reefs and islands. These are associated with a range of high energy exposed open ocean coasts through to the protected low energy shorelines of the upper gulfs.

The immediate impact of any sea level rise will be to increase the magnitude and frequency of extreme tides and levels of storm erosion, although the effects of this will vary greatly around the coast. The least vulnerable areas will be the resistant rocky coasts of the Fleurieu Peninsula, Kangaroo Island and Eyre Peninsula but there is likely to be greater erosion on the more predominant softer aeolianite and Tertiary limestone rocky coasts. The actual rate of cliff or bluff retreat on these coasts will vary with factors such as rock resistance, structure, the presence or absence of shore platforms or nearshore reefs, exposure to wave action, and tidal range (Bird 1993).

On the sandy coasts which represent about half (1900 km) of the South Australian coast are likely to have a variable response because of differing rates of littoral drift, onshore-offshore sediment movement, and sediment size variability. The high energy beaches of

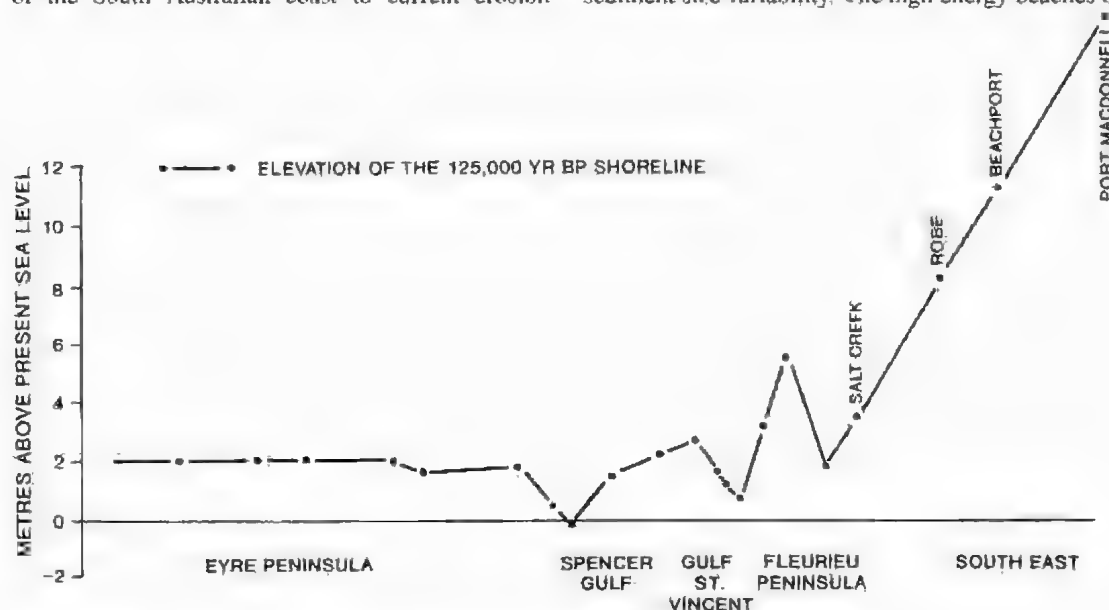


Fig. 3. Changing elevation of the last interglacial shoreline (125000 yr BP) in South Australia.

the Younghusband and Sir Richard peninsulas for example are backed by an extensive dune coastal barrier system which would be vulnerable to increased storm attack with elevated sea levels. Coastline retreat and the development of dune blowouts is likely to cause a migration of the barrier towards the Coorong. As this occurs underlying calcareous and back barrier muds would become exposed causing variable rates of retreat. In addition raised water levels will impact on the Coorong.

In contrast, the metropolitan sandy coast lacks the extensive backing dune barriers of the south-east. Urban encroachment across the frontal dune together with extensive protective works have necessitated a sand replenishment program to maintain the beaches. Elevated sea levels are likely to have greatest financial impact in this area where storm protection will need to be upgraded together with an increased sand replenishment programme, if the metropolitan beaches are to be maintained. To the north of metropolitan Adelaide, land subsidence has already been noted for the Port Adelaide area. Elevated sea levels will exacerbate the rate of relative sea level rise causing mangroves to advance further inland and changes to ecological zonations of the inter-tidal and supra-tidal biota. In some places mangrove advance may be restricted by artificial embankments resulting in mangrove die back.

In the gulf regions, similar displacement of ecological communities such as seagrasses, mangroves and samphires would be pronounced along the low gradient coasts. This rapid coastal retreat would be associated with reactivation of tidal swamps, localised flooding of the coastal plains and erosion of beach ridge systems.

In other parts of the coast, an elevated sea level is likely to cause flooding of low lying land, enlargement of coastal lakes and/or connection of some lakes to the sea, raised groundwater levels and alteration to estuarine environments. South Australia has few estuaries although there could be major implications for urban development adjacent to estuaries such as the Onkaparinga and the Port River. In the case of the Port River estuary, approximately 25% of the nearby urban development is currently below high water. Elsewhere, potential impacts on the Murray River residual estuary (artificially constrained by the construction of barrages) may be less significant for urban areas but could have major implications for the operating levels of the barrages and affect the management of the Murray Mouth and lower Murray Lakes region (Harvey 1988).

Assessing vulnerability: The IPCC common methodology

In late 1991 the Coastal Zone Management Sub-group of the IPCC released its "Common Methodology" for the assessment of vulnerability of coastal areas to sea level rise (IPCC 1991). An advisory group comprising the United Nations Environment Program (UNEP) and 12 nations initiated a series of case studies to examine

appropriate national response strategies and implementation requirements for coasts vulnerable to sea level rise. The Common Methodology for assessing vulnerability comprises the following basic steps:

- 1 Delineation of case study area and specification of accelerated sea level rise and climate change boundary conditions.
- 2 Inventory of study area characteristics.
- 3 Projection of relevant development factors.
- 4 Assessment of physical changes and natural responses.
- 5 Formulation of response strategies and assessment of their costs and effects.
- 6 The assessment of the vulnerability profile and interpretation of results.
- 7 Identification of actions to develop a long term coastal zone management plan.

The assessment process, using these steps, is explained in detail together with tables and checklists to assist in the compilation of data in a consistent manner (IPCC 1991).

The Common Methodology approach was found to be deficient by Kay *et al.* (1992) in their Western Australian case study. They suggest that there are problems in the biophysical structure of the assessment and also in the engineering dominated approach to cost benefit response mechanisms. They also indicate that there is an essential step between the assessment of impacts and the formulation of a policy response to reduce those impacts. In Western Australia, the policy formulation includes inter- and intra-government liaison, public consultation, and political consultation, eventually leading to strategic coastal zone management. However, the fact that strategic coastal engineering decisions are part of wider State and regional planning issues, means that preference may be given to reactive coast protection strategies for short term erosion problems rather than long-term coastal strategies related to sea level rise. This type of problem highlights some of the difficulties in developing a common approach strategy encompassing biophysical, administrative and legislative factors (Kay *et al.* 1992).

In South Australia, the IPCC Common Methodology has yet to be tested but it is likely that bureaucratic and political problems are currently compounded by uncertainty with the review of the 20 year old *Coast Protection Act*, debate over cost sharing for coastal management between State and local government.

Discussion

Appropriateness of current South Australian policy

Initial estimates of the current rate of sea level rise obtained by averaging tide gauge data from around the world have been reducing. The principle reason is the recognition that land level changes need to be removed

from the tide gauge data before they can be used for this purpose. Underlying, unrecognised neotectonic effects remain the main reason for the geographic variability in secular tide gauge trends. A global sea level rise cannot be expected to be detected until adequate corrections are made for these effects at each tide gauge site. With consensus estimates of predicted sea level rise now down to 0.65 m over the next 100 years, these neotectonic effects will be determining factors in overall local sea level behaviour. In the gulfs, any rise of sea level will be mitigated by ongoing isostatic upwarp of up to 0.8 mm yr⁻¹. In the South-East, tectonic uplift will be a mitigating circumstance. In major towns, particularly where wetland reclamation has occurred, or excessive groundwater withdrawal is taking place, any greenhouse sea level rise will be exacerbated by land subsidence effects.

In the absence of accurate geodetic or altimetric data, the geologic record can be used to obtain first-order estimates of land level changes. In South Australia, the coastal record has produced some useful results that go some way towards explaining the variability of sea level change documented by tide gauges. However, there remains a pressing need for local and global crustal scale geodetic control of all tide gauge sites. In addition, a geographically suitable spread of tide gauge sites is required to account for the scale and variability of neotectonic processes. In South Australia, these tide gauge sites are required within the gulfs as well as along the oceanic coastline and offshore islands.

The implications of this for South Australia's coastal policy are twofold. First, it highlights the need for accurate local sea level data which are then corrected for neotectonic and anthropogenic factors. The preliminary corrected sea level trend figures presented in this paper indicate that the current rate of sea level rise in South Australia has generally been overestimated apart from two sites where the reverse is true. Second, this South Australian case study provides support for

Pirazzoli's concerns that the global averages for current eustatic sea level rise may also be overestimated. The compounding effect of uncorrected global sea level rise trends added to uncorrected local trends will produce inaccuracies in the sea level trend data upon which the policies are based.

In addition the uncertainties surrounding climate change predictions and the associated sea level response necessitate the adoption of the precautionary principle allowing safety margins for building levels and erosion set-backs. Although this may have major cost implications for coastal development, it is unlikely that a greater precision for climate change models and sea level response will be reached in the near future. However, it is possible to reduce some of the uncertainties of current sea level measurements by correcting sea level data for neotectonic and anthropogenic influences.

Conclusions

The data presented in this paper indicate the need for taking neotectonic and anthropogenic factors into account for calculating current rates of sea level rise. The secular trend obtained from tide gauge data is only a relative sea level trend since the tide gauge cannot distinguish between a real rise of sea level and crustal subsidence at the site. This paper indicates that the current rate of sea level rise based on South Australia tide gauge data has generally been overestimated apart from two sites where the reverse is true. It is apparent from this paper that all tide gauge sites must be corrected for vertical crustal movements before any conclusions are drawn regarding local or global sea level change. The implications of this for South Australian coasts are that adjustments to sea level trends should be made before any vulnerability assessments are conducted. It may also be possible to revise policy guidelines based on the revised sea level trend data.

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CLIMATIC CHANGE AND ITS IMPLICATIONS FOR THE AMPHIBIAN FAUNA

*By MICHAEL J. TYLER**

Summary

Tyler, M. J. (1994) Climatic change and its implications for the amphibian fauna. Trans. R. Soc. S. Aust. 118(1), 53-57, 31 May, 1994.

The dependence of frogs upon moisture makes them highly sensitive to environmental conditions. The South Australian frog fauna includes 28 species which collectively and individually experiences a wide temporal range of temperature and available moisture. Any climatic change involving warmer and moister conditions is likely to enhance their distribution and abundance.

Key Words: Frogs, moisture, distribution, South Australia.

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Introduction

The relevance of the study of frogs in any evaluation of the impacts of climatic change hinges upon recognition of the dependence of these animals upon moisture. Nevertheless the survival of frogs throughout the period that witnessed the entire evolution of all other terrestrial vertebrates, demonstrates the capacity of frogs to survive massive environmental changes.

The complete extent of the diversity of the modern frog fauna is unknown: Duellman (1993) estimates a total of 3967 species at 31.xii.91, and numerous species have been described subsequently. In Australia the current total is 203, but many more await description.

Despite the success and longevity of frogs as an evolutionary lineage they remain dependent upon moisture because of the relative permeability of the skin and (in most species) the need to deposit eggs in free bodies of water.

It follows that frogs are highly sensitive indicators of environmental pollution and, equally, that they contribute an early warning system in terms of detecting environmental changes.

Any climatic change in South Australia at a regional or total level is likely to impact upon the distribution of species, and upon the number within this State.

South Australian frog fauna

Currently 28 species of frogs have been reported from South Australia. The largest number of species in any area (11) is to be found in the lower southeast which is also the area of highest rainfall. However comparable numbers are found in the arid northwest (9) and northeast (10) (Table 1).

The northwest and the northeast are also the portions of South Australia where numerically and proportionately there are the most species not shared with other areas (Table 1). In each instance these "unique" species are known within South Australia

from fewer than six localities, and each species is more widely distributed outside the State. Numerous frog species in South Australia are at the geographic limit of their distribution, and climatic change may have a dramatic influence upon their persistence or abundance.

TABLE 1: Geographic characteristics of South Australian frog fauna.

Geographic Area	Number of species	Species confined to that area	Known from less than six localities
Northwest	9	5	5
Northeast	10	5	5
Flinders Ranges	5	1	0
Eyre Peninsula	3	0	0
Yorke Peninsula	2	0	0
Mt Lofty Ranges	7	0	0
Murray Valley	9	3	0
Kangaroo Island	6	0	0
Lower southeast	11	4	0
Nullarbor Plain	2	0	0

Impact of Rainfall

Although the amount of rainfall and its reliability are not the only factors influencing frog distribution, the generality can be made that the persistence of moisture at or near ground level is most important.

To predict faunal impact in South Australia it is pertinent to examine a geographic area in which there is a progressive increase or decrease in rainfall along a latitudinal gradient. The one area in Australia in which this requirement is met is the Northern Territory, where there is a progressive reduction in annual rainfall from north to south (Fig. 1).

The Northern Territory model

Based upon the distribution patterns of the 42 species then known from the Northern Territory plotted by

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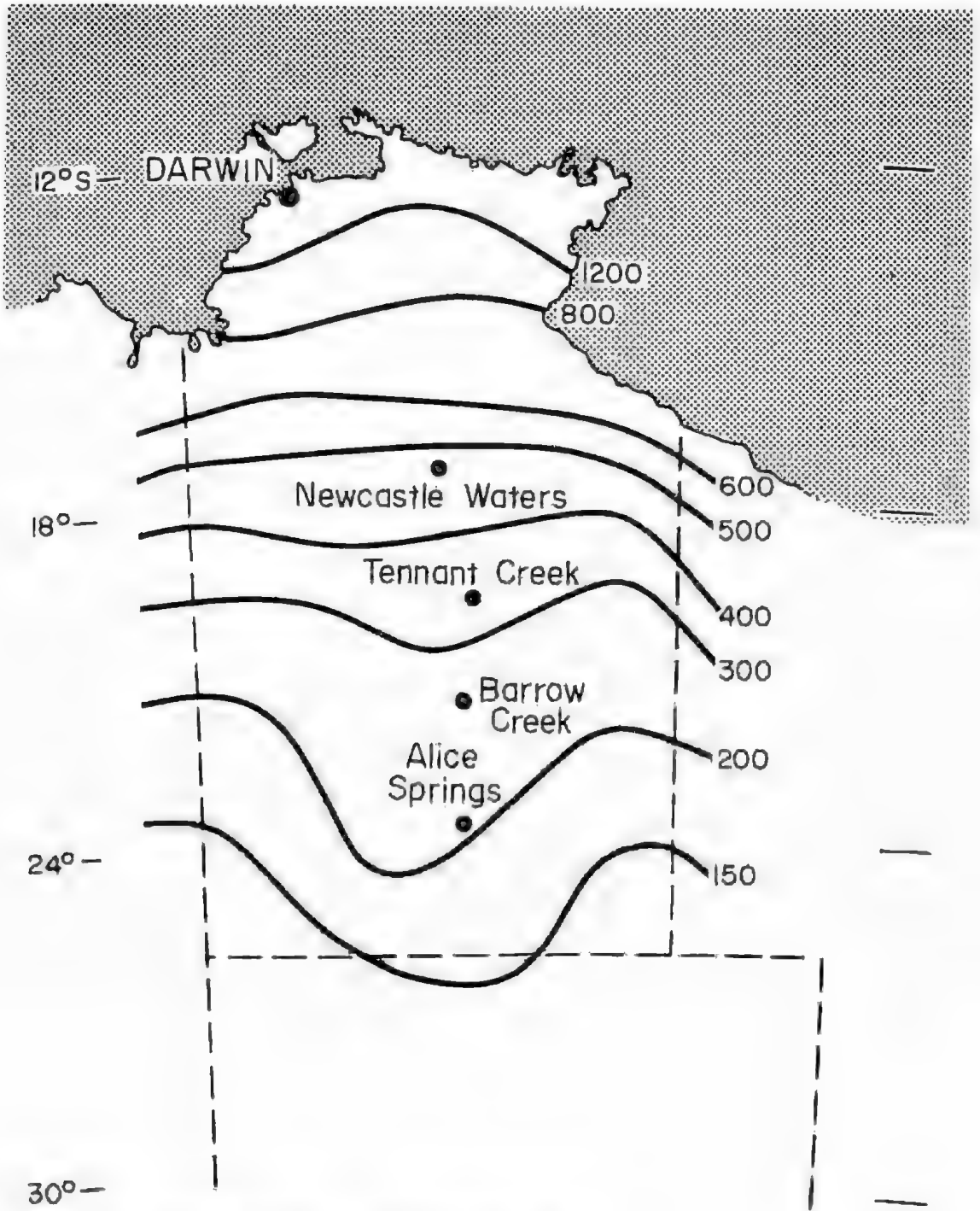


Fig. 1. Northern Territory showing latitudes, isohyets and major centres.

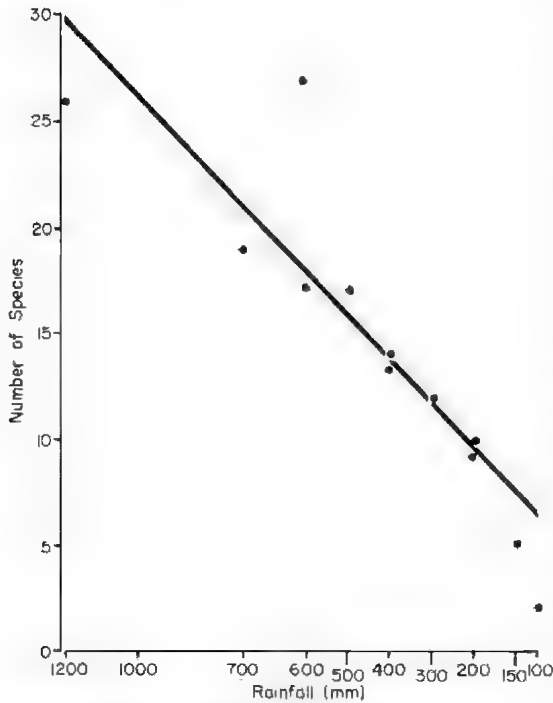


Fig. 2. Number of species plotted against isohyets ($r = .750$).

Tyler & Davies (1986) there is a distinct association between rainfall and the number of species (Fig. 2) within rainfall zones where there is 100-500 mm per annum. At rainfalls higher than 500 mm the trend is not apparent, but the geographic area involves Arnhem Land which has been largely inaccessible to collectors. I anticipate that the totals for the more northern latitudes will increase when zoological exploration becomes possible.

Because of their dependence upon having access to sources of moisture, the evolutionary capacity of body size and mass of frogs are closely linked to the reliability of sources of moisture. Species of small size have a surface area to mass relationship that is fitted to reliable sources of moisture. Conversely the capacity to withstand xeric conditions requires that the surface area from which water is lost is, by some means, reduced. Effectively large, bulky frogs are best equipped for xeric conditions.

Although the length of the body bears no fixed relationship to body mass, it is the standard expression of size ($S-V$ = snout to vent length). In Australian species there is marked sexual dimorphism: males are always smaller than females (except for the eastern Australian species *Adelotus brevis*). To examine any geographic trends in size I have used a median

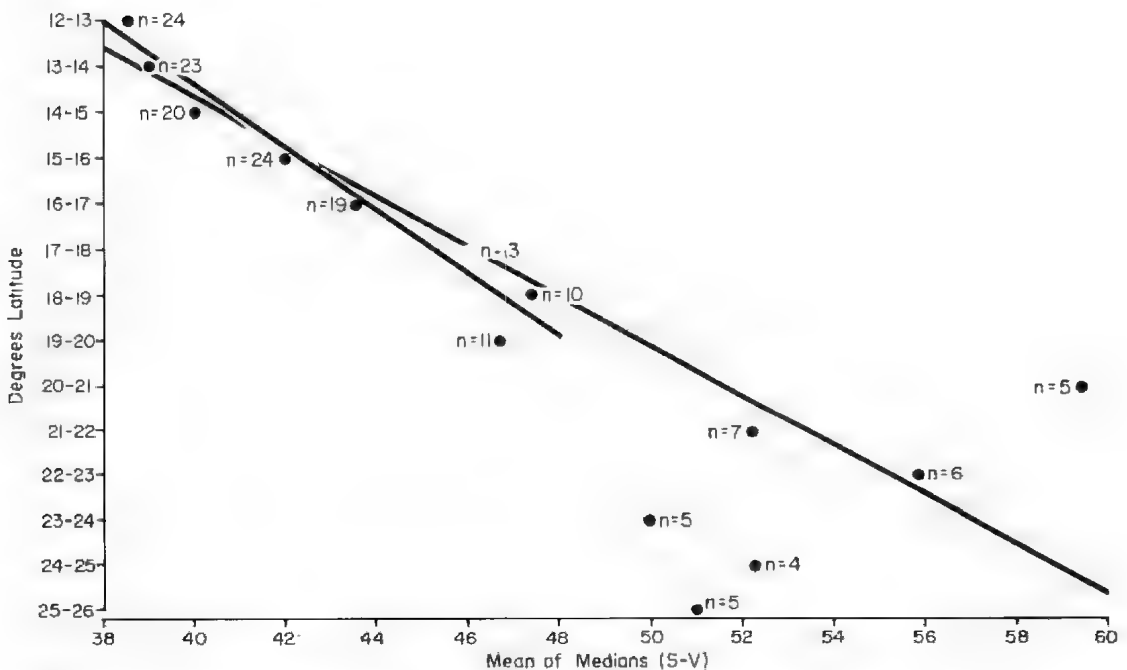


Fig. 3. Number of species occurring within particular latitudes (boundaries at single degree positions) plotted against mean of medians of snout to vent length (S-V). Two linear regression lines have been plotted: one between 12° and 20°S ($r = .948$), the second between 12° and 26°S ($r = .975$).

measurement, being the midpoint between the size of the smallest adult male and largest adult female. The first of these analyses followed the standard 1° latitudinal divisions (Fig. 3). The second involved similar latitudinal divisions but separated at the intermediate 0.5° divisions (Fig. 4). Essentially the results are similar: small species are associated with high levels of moisture, and in arid areas larger species predominate.

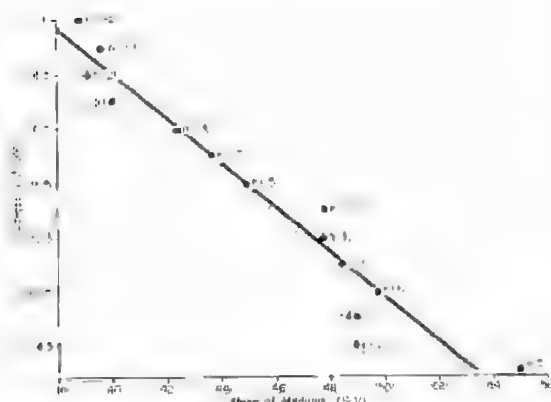


Fig. 4. Number of species occurring within particular latitudes (boundaries at half degree positions) plotted against medians of snout to vent length (S-V). Regression line $r = .921$

The overall lifestyle of frogs also is reflected along these north-south transects of decreasing available moisture. In terms of the size of the individuals there is a shift in the predominance of small species to larger ones associated with rainfall. Equally there is a distinct change in the overall lifestyle of these same species, such that the terrestrial/aquatic mode shifts from more than 50% in the extreme north of the Northern Territory to zero at 21° latitude south.

Existing geographic trends in South Australia

Within South Australia there is a direct association between the number (and diversity) of species and geographic area, but without the latitudinal decrease from the arid north to the moist south. Instead there are pockets of species, each of which has its own unique features.

For example any gradient is destroyed by the presence of a wet refuge like that of the Coongie Lakes system in the northeast of this State — an intrusion of an area wholly atypical within a broad zone of low and irregular rainfall. The Coongie Lakes frog fauna is particularly rich, but not permanent because of the period of drought. It has been suggested that the northeast of the State presents a dynamic situation in which there is contraction and expansion of populations according to the availability of moisture and repeated

transportation of species from southern Queensland (Tyler 1990: Fig. 3).

The River Murray presents a further dimension because it constitutes a route for the introduction of species from the east. *Litoria peroni* and *Criidula parinsignifera* enter the State by this means, and are confined to its vicinity.

The toadlet *Pseudophryne occidentalis* has an extensive distribution in Western Australia, whereas in South Australia it has been found only at Victory Well in the Everard Ranges in the northwest. The existence of species within such restricted areas is of significance to palaeoclimatic interpretation. Because of the small geographic area to which it is confined, the dependance of the species upon moisture, and the existence of more arid conditions around the area, it can be inferred that since the time of dispersal to that site, it has not been more arid there than at present.

With the exception of *Criidula riparia* which is wholly confined to the Flinders Ranges, every species in South Australia has a more extensive distribution beyond the State boundaries. In fact the percentage of endemism in South Australia is less than in any other Australian State.

The implications of climatic change

The climatic variables that influence the geographic distribution of Australian species of frogs are very poorly known. Brattstrom (1970) was the first to demonstrate an association in montane species between altitudinal location and tolerance to temperature fluctuations. In particular he indicated that the species occupying the cooler habitats had the least capacity to adapt to a change in thermal regime.

Unfortunately the climatic variables that have particular influence upon the spatial distribution of frogs are, at best, inferred rather than demonstrated. For example, what is the limiting factor of the distribution of the tree frog *Litoria rubella* which extends as far south as Wilpena Creek in the Flinders Ranges?

This species ranges across the entire northern half of the continent, principally within the area of summer rains (Fig. 5). A commensal species, it is clearly capable of adapting to changing environments. It can be assumed that a climatic change producing warmer and moister conditions will enhance the geographic range of *L. rubella*.

Perhaps the most significant influence of climatic change will be the creation of more aquatic breeding sites and the persistence of these sites for longer periods. Together these factors will modify habitats in a manner that is advantageous to frogs. Hence the Coongie Lakes are likely to become more persistent, and the fauna there more stable in a temporal sense than at present.



Fig. 5. Geographic distribution of *Litoria rubella*

Conclusion

Any climatic change that results in a moister and warmer climate in South Australia is likely to enhance the geographic distribution of the constituent species. This can be assumed because of the wide range of temperatures experienced already by South Australian species, and the fact that a warmer and moist regime will ameliorate the existing seasonally harsh environmental conditions.

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CLIMATE CHANGE AND ITS IMPLICATIONS FOR THE TERRESTRIAL VERTEBRATE FAUNA

By PHILIP STOTT

Summary

Stott, P. (1994) Climate change and its implications for the terrestrial vertebrate fauna (1994). Trans. R. Soc. S. Aust. 118(1), 59-68, 31 May, 1994.

A limited number of studies of the biology of a variety of species of terrestrial vertebrates is used to speculate about their responses to climate change as predicted by global circulation models. Dramatic changes in the distribution and abundance of animals in Australia that has already occurred consequent to European settlement is noted. Speculation about the impact of climate change on the relative abundance of mammals and reptiles, range changes of kangaroos, rabbits in arid areas, food security of the Spinifex Hopping Mouse, competition between two species of skinks, and disease transmission is included. Nest-site selection by tortoises and social structure of foxes are given as two examples where behavioural plasticity demonstrates some capacity to cope in situ with the effects of climate change, but the ability of most terrestrial vertebrates to track rapid climate change across different substrates is questioned. Reservations are expressed about the knowledge base upon which the speculations are based. For very few species is a suite of studies available to compare detailed data on distribution and abundance with climate over a wide geographical range, backed up with biological information sufficient to explain the mechanisms by which the species interact with their environments.

Key Words: Climate change, mammals, reptiles, Testudines, abundance, distribution, rainfall, drought, disease, *Macropus giganteus*, *Macropus fuliginosus*, *Oryctolagus cuniculus*.

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Introduction

Some 6000 years ago, within the span of 100 years, the vegetation at Cold Water Cave, Iowa, changed from forest to prairie (Dorale *et al.* 1992). The changes were associated with a temperature rise of c. 3°C, and with such a complete change in vegetation structure must have come a profound change in the vertebrate fauna of the locality. It may be, during the next century, that similar dramatic changes in biota will result from an anthropogenically-enhanced "greenhouse" effect. The terrestrial vertebrate fauna of Australia has already undergone profound changes as a consequence of European settlement (Recher & Lim 1990); climate change would compound the impacts of introduced competitors and predators, destruction and fragmentation of habitat, altered fire regimes, hunting, and diseases.

Realistic predictions about the impact of climate change on the distribution and abundance of terrestrial vertebrate species require a foundation of information from several sources. Essential are detailed forecasts from climatologists; predictions about changes in the distribution, composition, and productivity of plant communities and other elements of food webs; and detailed information about the present distribution, abundance, physiology, and ecology of vertebrates. The temporal scale of possible changes should also be considered.

The sentiments expressed in this paper are complementary to those expressed in essays by Arnold (1988), Busby (1988), Graetz (1988), Main (1988), and Possingham (1993). The paper augments previous contributions by exploring some examples of the mechanisms by which climate change might affect vertebrates. It is a speculative paper; the scenarios are presented with the intent of illustrating the level of complexity, rather than making confident predictions about the outcome. The predictions are weakened because a single study of a local population over a short period of time is not necessarily representative of the biology of a species during all seasons and over the whole of its range (see Kemper *et al.* 1987), and the range and habitat of a species as observed to date do not necessarily represent accurately the realised environmental niche of the species, nor this in turn its fundamental niche (Possingham 1993). In addition, the predictions of global climate models are not considered to be reliable at the regional level (Gordon *et al.* 1992). As the number of logical steps increases, so the errors are summed.

The paper reviews those climatic predictions of particular importance to animals, uses some examples to explore the mechanisms by which climate change might affect terrestrial vertebrates, then examines the capacity of animals to cope with the predicted changes.

Predicted climate changes

Evidence from climate models indicates that emissions of "greenhouse" gases into the atmosphere

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will cause global warming of 0.3 (range 0.2–0.5) °C per decade, and associated changes in patterns of precipitation (Houghton *et al.* 1992). Whilst the general predictions of the models are broadly accepted, the issue is complicated by the lack of clear observational evidence of changes attributable with certainty to an enhanced 'greenhouse' effect. On examining records of meteorological observations, Nicholls & Lavery (1992) were not able to identify any clear trends in rainfall at reliable meteorological stations in South Australia up until 1988. Although Burrows & Staples (1991) note a warming trend in South Australia since 1950, they cautioned that the trend was 'close to the bounds of past experience'. Models are not consistent in their predictions of seasonal changes in temperature patterns for South Australia (see Boer *et al.* 1992; Gates *et al.* 1992); at the present state of refinement of the general circulation models such uncertainties in timing, magnitude, and regional patterns are well recognised (Houghton *et al.* 1992).

Rainfall has a major influence on food supply for vertebrate species, particularly in arid areas. Haarsma *et al.* (1993) predict a global increase in tropical disturbances. At present, some of these disturbances extend into northern South Australia as tropical-extratropical cloudbands (TECBs), and as a result heavy rain falls on an average of nine days per year (Kuhnel 1990). However, the distribution and extent of the rainfall is erratic. Gordon *et al.* (1992) cautiously report the results of simulations which indicate changes in daily rainfall intensity across Australia, particularly in summer, in the form of increases in the frequency of heavy (12.8–25.6 mm, *c.* 31%; >25.6 mm, *c.* 95%) rainfall days, an *c.* 15% decrease in the frequency of light (<6.4 mm) rainfall days, and a decrease in the number of rain days. Whetton *et al.* (in press) review the predictions of five global circulation models: four predict increasing summer rainfall over the whole of South Australia (all five predict increasing summer rainfall over much of the far north), and four predict a decrease in winter rainfall over most of South Australia.

A weakness of the models is that they do not take into account all major known influences on climate. The El Niño–Southern Oscillation (ENSO) phenomenon is not coupled with the major global circulation models (including the CSIRO9 model) despite its influence on variability of rainfall in Australia (Whetton *et al.* in press). ENSO is of particular importance in the recruitment of many arid zone species (Austin & Williams 1988; Graetz *et al.* 1988). The influence of ENSO needs to be considered in addition to changes predicted to accompany the enhanced greenhouse effect (Walker *et al.* 1989). The issue is further complicated because ENSO itself may be affected. If increased CO₂ works to equalise temperatures in the waters off

the eastern and western Pacific Ocean, ENSO would be weakened (Rind 1991), thus tending to reduce climatic variability in eastern Australia and countering to some extent the predictions outlined above.

Direct effects

Direct effects of climate on vertebrates should be more readily elucidated than would be the case with indirect effects. Two examples are presented of direct effects of climate on reptiles. The first is the process of temperature-dependent sex determination, and the second is the influence of temperature on the distribution of testudines (turtles and tortoises). Both examples demonstrate that the knowledge base is inadequate even in this more straightforward category.

Temperature-dependent sex determination

Temperature-dependent sex determination (TSD) has been demonstrated in many species of testudines (e.g. Mrosovsky *et al.* 1984), crocodilians (e.g. Webb *et al.* 1983), an agamid (Charnier 1966 *vide* Bull 1980), and a gekkonid (Wagner 1980). Slight (<2°C) departures from pivotal incubation temperatures may result in entirely male or entirely female sexual phenotypes, even in some of the species which have heteromorphic sex chromosomes (Servan *et al.* 1989). Some species have two thresholds, with males resulting from intermediate and females from extreme incubation temperatures (Yntema 1976; Webb & Smith 1984). TSD has been demonstrated to occur in an Australian crocodilian (Webb *et al.* 1983), an Australian freshwater/estuarine testudine (Webb *et al.* 1986), and Australian marine testudines (Limpus *et al.* 1985). In contrast, it does not occur in several Australian freshwater testudines, including species found in South Australia (Georges 1988; Thompson 1988a). Preliminary studies suggest that TSD occurs in at least four Australian agamids (G. Johnston *pers. comm.*).

The influence of environmental temperature on sex ratios is a mechanism by which climate change can directly affect the distribution of reptiles. Species with TSD would be more susceptible to rapid climate change than species without TSD. Webb & Smith (1984) noted variation in sex ratios of *Crocodylus johnstoni* hatchlings in the field, and speculated that it was due to the interaction between TSD and geographic differences in mean air temperatures. In a warmer climate, the effect might be to skew the sex ratio completely, blocking reproduction, and thus leading to the local extinction of the species. Such a scenario has been advanced by Pieau (1982) as a possible reason for the extinction of many Mesozoic reptiles.

Distribution of testudines

Testudines, which require external sources of heat for metabolic activity, are limited in latitudinal distribution by temperature. However, mean annual temperature is far too crude a measure to predict limits to distribution. Length of the growing season has been generally accepted as a limiting factor, since at the latitudinal limits of distribution adults may not have enough time to accumulate sufficient energy reserves to survive the winter (MacCulloch & Secoy 1983). Alternatively, distribution may be limited by the ability of hatchlings to survive overwintering in the nest (Breitenbach *et al.* 1984; Congdon *et al.* 1987). Ohband & Brooks (1987) suggest that a critical factor is temperature during the maturation of twa, which requires the accumulation of heat units over spring sufficient for successful reproduction. I suggest another possibility; that distribution is limited by the probability of ambient temperatures being sufficiently high during the nesting season to permit the energy expenditure necessary in digging the nest chamber, an activity recognised as being energetically demanding (Congdon & Gatten 1989).

To predict the effect that climate change would have on a species requires detailed knowledge both of the nature of the change in climate and of the mechanisms by which climate change would affect a species. In testudines, we need to know which of the above hypotheses is acceptable before we know whether to examine number of days between threshold temperatures, nadir winter temperatures, number of spring days above a temperature threshold, or the probability of occurrence in spring of spot temperatures above a threshold.

Indirect effects

Effects mediated by other factors are inherently more complex than direct effects. Attempts at predicting changes in animal distributions based on detailed analyses of complex mechanisms which include consideration of matters such as physiology, population dynamics, interspecific interactions, behavioural changes, and microhabitat conditions are fraught with potential for error. An alternative is to identify a smaller suite of influences which drive the system and determine the end result. Nix (1982) saw climate as the major determinant of the distribution of terrestrial organisms, and several authors have used various climatic indices to explain the diversity and abundance of particular Australian biota. Of particular value are those rare studies which compare detailed data on distribution and abundance with climate over a wide geographical range. Both mechanistic and deterministic explorations follow.

Relative abundance of mammals and reptiles

Arid Australia already has a more diverse and abundant reptile fauna than arid areas in North America and Africa (Pianka 1985). In part, the diversity and abundance of the reptiles is attributed to the high variability of rainfall which is a feature of the Australian inland (Morton & James 1988). Proposed changes in climate might therefore be expected to lead to an increase in the diversity and abundance of reptiles relative to mammals.

Not all mammals would necessarily be adversely affected. For the large arid areas of Australia, net annual productivity and hence the carrying capacity expressed as total biomass of vertebrates is related to annual rainfall (Burbidge & McKenzie 1989). However, the species composition of the total biomass is largely determined by the predictability and distribution of the rainfall, rather than its amount. Patchy rainfall favours birds, bats, and mobile large mammals such as kangaroos (Burbidge & McKenzie 1989) which are physically capable of moving long distances to environments made favourable by recent heavy rains. Irregular rainfall favours reptiles, which have very low field metabolic rates relative to mammals (Nagy 1987) and can survive for long periods without food (Morton & James 1988). A change in rainfall patterns to fewer days with rain, a lower probability of light rainfall, and an increase in the frequency of heavy rainfall would not have a great impact on mobile animals, but would favour reptiles over small mammals. Small mammalian cellulose-dependent herbivores would be particularly disadvantaged; they are vulnerable because their energy intake is limited by their gut size. This represents a similar proportion of the size of the individual as in larger animals, but the energy expenditure for maintenance of body temperature must be relatively higher than for larger mammals which have a lower surface area to body mass ratio (Morton 1990). They are also limited by their restricted mobility in their ability to exploit a patchy environment; and they are most vulnerable to competition from rabbits (Burbidge & McKenzie 1989; Morton 1990).

It could be argued that the balance between the diversity of reptilian and mammalian species as at the time of European settlement was determined in some prior, more severe period of aridity (such periods are known from prehistoric times—see Singh 1981), and therefore the balance would not be affected by a further increase in temperature and in the variability of rainfall. Further, any mammals which might have been affected are already extinct as a consequence of European settlement. The counter argument is that effective aridity in the future may be more extreme than in recent evolutionary time. Climatic aridity (wherein increased evaporation is in excess of increased rainfall) may be compounded by 'emulated aridity' because of the

consequences of the removal of primary productivity from the arid system in the form of livestock and livestock products (Burbidge & McKenzie 1989), and the sequestration within the arid system of primary productivity and nutrients in the tissues of livestock and rabbits. Thus the resources available to native vertebrates would be significantly diminished, particularly during the resource "bottlenecks" of droughts, and in drought refuges (see Morton 1990).

Range changes of kangaroos

The responses of kangaroos can perhaps be predicted with a little more confidence than those of other vertebrates. Many studies of kangaroos have been undertaken, including thorough studies of their distributions (Fig. 1a) as part of the basis for managing populations which are commercially harvested.

Caughley *et al.* (1987) have demonstrated that the distribution of three species of kangaroos is, in the major part, determined by climate. Whilst the distributions are directly determined by land use and the availability of food, water, and shelter, these attributes are in turn greatly influenced by climate. The distributions of the two grey kangaroos, the Eastern Grey Kangaroo (*Macropus giganteus*) and the Western Grey Kangaroo (*M. fuliginosus*), are closely associated with the seasonality of rainfall; they overlap in areas of uniform seasonality of rainfall, but *M. giganteus* occurs in areas where summer rainfall predominates, and *M. fuliginosus* occurs in areas where winter rainfall predominates. The Eastern Grey tolerates higher seasonal temperatures than the Western Grey provided

that there is summer rainfall. Both require a heterogeneous habitat with shelter being an important component (see Hill 1981, Cairnes *et al.* 1991). The distributional data have been used by Walker (1990) to develop an integrated modelling and mapping system which could be used to predict and map changes in distribution consequent to climatic change. Caughley *et al.* (1987) suggest that climate change in the past has influenced the distribution of macropods: it is therefore reasonable to use their conclusions to predict the distributional responses of these three species to future climate change.

If, as predicted (above), the winter rainfall zone contracts to the south and temperatures rise, the distribution of the Western Grey Kangaroo would also contract to the south (Fig. 1b). Perhaps more remarkable might be changes to the distribution of the Eastern Grey Kangaroo. At present the species occupies two small and widely separated areas in South Australia, but these are minor projections into this State of a distribution whose western boundary runs along or just to the east of the State's eastern borders (Caughley *et al.* 1984). *M. giganteus* could extend a considerable distance to the west of its present distribution, and hence across the north of South Australia to occupy suitable habitats in the northern part of the present range of *M. fuliginosus*, if certain conditions are met. They are that summer rain becomes more common in northern South Australia, that reliable water is provided by increased frequency of heavy rainfall and/or livestock water supplies, and that habitat heterogeneity persists in the face of climate change.

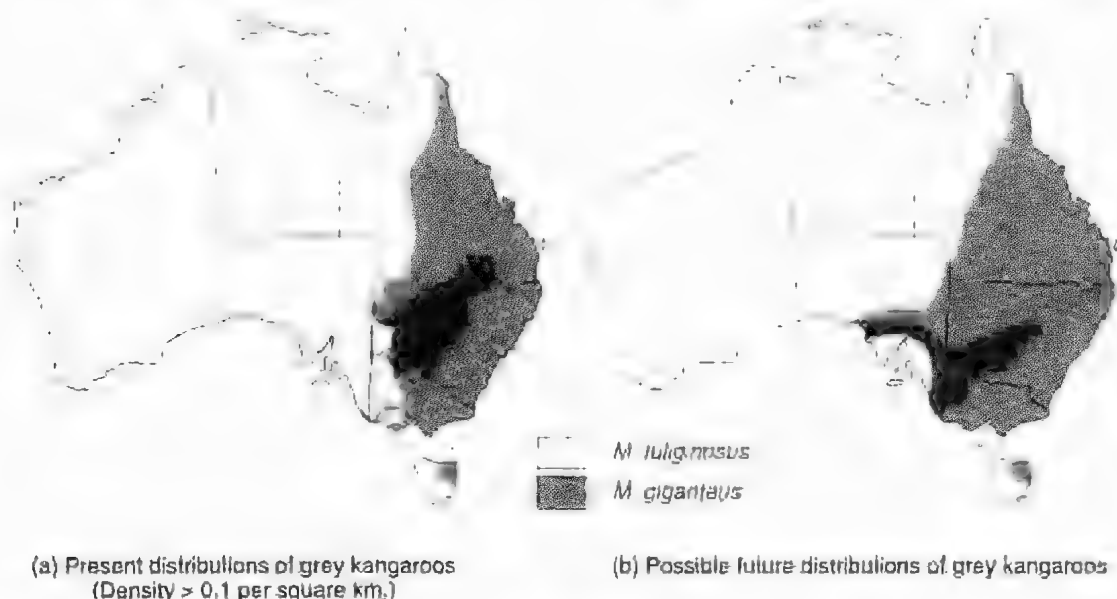


Fig. 1. (a) Present distributions of grey kangaroos. (b) Possible future distributions of grey kangaroos. Adapted from Cairnes *et al.* (1991), Caughley & Grigg (1981), Caughley *et al.* (1983), Caughley *et al.* (1984), Short *et al.* (1984).

Survival of rabbits in arid areas

In arid Australia, the European Rabbit *Oryctolagus cuniculus* is decreasing the probability of survival of small perennial plants during droughts, and having a profound effect on the recruitment of some species, sufficient in time to eliminate them from the landscape (Lange & Graham 1983; Cooke 1987). The response of the rabbit to climate change is therefore of particular importance.

Historical records show that rabbits in arid areas have been severely reduced in numbers during past droughts (Griffin & Friedel 1985), and may, under drought conditions, become extinct over large areas (Myers & Parker 1975). Recruitment is most unlikely under drought conditions (King *et al.* 1983), and prolonged droughts such as the 1938-64 and 1925-38 droughts at Alice Springs (Griffin & Friedel 1985) test the longevity of the species (see e.g. Dunsmore 1974). Even so, a few rabbits survive in refuges. The quality of the refuges is determined by their ability to harvest and store water and nutrients flowing from larger areas of the landscape (Morton 1990) such that run-off from light rainfall is sufficient to stimulate some plant growth during the drought period (Ludwig 1987). At Wilchitlie, South Australia, Cooke (1982) noted that a sharp fall of little more than 5 mm of rain might be sufficient to yield run-off which, if concentrated along drainage lines, would ensure that succulent food in the form of chenopod shrubs would be available to rabbits living in warrens along those drainage lines. Once heavy rain falls (>20 mm near Carnarvon, Western Australia, King *et al.* 1983), rabbits begin to breed, and can expand from the refuges to recolonise the bulk of the landscape.

Heavy rainfalls are rare in the Australian arid zone; whole years may pass without a rainfall event ≥ 12.5 mm (Stafford Smith & Morton 1990). Light falls are more common, but it has been predicted (see above) that the heavy falls would become more common, and light falls somewhat less common. Hence, droughts are likely to be shorter in duration, but the refuges which sustain the residual rabbit population during droughts would be a little less reliable. With a coincident rise in temperature exacerbating the severe physiological stress experienced by rabbits under present summer conditions (Hayward 1961), local extinction becomes more likely during droughts, but, with decreased return times for heavy rain, plagues might be expected more frequently in those areas where rabbits survive.

Vegetation changes consequent to the increased variability of precipitation might not favour rabbits. Rabbits are found in chenopod shrublands, but the majority of the feed is provided by the short grasses and forbs between the shrubs; the chenopods are eaten only during droughts (Hall *et al.* 1964; Griffin & Friedel 1985). Under conditions of increased climatic

variability, perennial plants would be favoured over ephemeral plants (Stafford Smith & Norton 1990), so rabbit populations could be expected to become less dense unless palatable perennial grasses such as *Themeda* sp. replaced annual grasses and forbs. Further exploration of this scenario would need to take account of a potential southern extension of the dominance of C_4 over C_3 grasses (Henderson *et al.* in press), the relative importance of C_3 and C_4 grasses to rabbits, and the implications for rabbits of a change in the seasonal distribution of rain towards summer rainfall in arid areas of South Australia.

Food security for Spinifex Hopping Mouse

Notomys alexis, the Spinifex Hopping Mouse, is widely distributed through sandy areas of northern South Australia, mainly in association with spinifex grasses (Watts & Aslin 1981). A major component of its diet is seed (Finlayson 1940), and from the carbohydrate in seed it is able to derive sufficient metabolic water to survive indefinitely; one female is known to have reared a single young without supplementary water (Baverstock & Watts 1975). Hence the regularity of seed production would influence survivability of *N. alexis* in northern areas of the State. Seed production may be influenced by soil moisture, temperature, and CO_2 levels, and two mechanisms by which *N. alexis* might be advantaged are explored.

Soil moisture is one of the most important climatically determined variables for grasslands (Pitcock 1993) and hence for species such as *N. alexis* which depend in large measure on grasses (MacMillan & Lee 1969). Walker *et al.* (1989) anticipate that mean soil moisture is likely to diminish in northern South Australia, although at present the reliability of predictions is questioned (Vinikov 1991; Pitcock 1993). More important for seed production are episodes of higher soil moisture following heavier rainfalls, which are predicted (above) to become more frequent. Thus pulses of seed supply may become more frequent, and support denser populations of *N. alexis*.

The rate of growth and the speed at which seed development occurs following rains may be accelerated. Imai *et al.* (1985) observed increased seed yield per plant for rice grown under enhanced greenhouse conditions. Gifford (1979, 1988) predicted that wheat yields in areas with more strongly seasonal rainfall would increase as a result of the enhanced 'greenhouse' effect, and that some grain growth would become possible under conditions of aridity which currently preclude any yield. The factor influencing yield was stimulation to plant growth by both increased CO_2 and warmer temperatures, which would result in a shorter growing season such that the grain was more likely to be filling under a favourable soil moisture regime. Enhanced efficiency of water use would also occur due to partial stomatal closure (Chaves & Pereira

1992). Thus droughts as perceived by *N. alexis* may be ameliorated by the supply of some seed when none would be otherwise be available.

Australian arid-zone soils are generally infertile (Morton 1990), and nutrient limitation may counter growth-stimulating mechanisms. Although seed production may be limited by the availability of phosphorus, nitrogen is less likely to be limiting for *C.* plants, but a likely corollary is that the protein content of their seeds would be lower (see Connry 1992). *N. alexis* would not be disadvantaged, as it is more likely to survive drought on low protein diets which obviate the need to expend water to dispose of waste nitrogen (MacMillan & Lee 1969).

Competition between *Ctenotus* species

Many of the 70 species in the scincid genus *Ctenotus* are associated with spinifex (Cogger 1992), and it is not unusual for several species to be syntopic, suggesting fine niche separation between them. If climate influences the niche separation, climate change may affect the balance between the species.

Ctenotus helenae and *C. pantherinus* are two species occurring sympatrically in the far north-east of South Australia; Pianka (1969) noted that they shared similar niches, and suggested that *C. pantherinus* would be excluded by *C. helenae* but for its reproductive capacity. James (1991a) found a high degree of dietary overlap between the two species, and noted that dietary overlap in *Ctenotus* was highest during the driest period of his study. There is evidence to suggest that the separation between these two species is based on their thermal responses; Pianka (1986) found *C. pantherinus* to have a lower mean body temperature than *C. helenae*, and James (1991b) speculated that *C. pantherinus* (and *C. brooksi*) can be active at winter temperatures which preclude activity by *C. helenae* (and other *Ctenotus* species). This permits *C. pantherinus* and *C. brooksi* to begin reproduction earlier than the other species. If activity at different temperatures is critical either for maintaining stable niche separation or for sustaining a mechanism of oscillating disequilibrium between the species, an increase in temperature during winter may result in competitive exclusion of *C. pantherinus* by *C. helenae* in those areas where they are sympatric.

Epidemiology

In stable ecosystems, there is generally a significant level of accommodation between host populations and disease-causing agents, particularly if they have co-evolved. However, transmission of infectious disease is a dynamic process, and in many cases is dependent on the capacity of the infectious agent to survive outside of the host. Helminth parasites often have obligatory larval stages which may survive for long periods on the ground, and thus be susceptible to climatic

influences. Should the climate change, the accommodation between the host and the parasite may be disturbed.

Amongst the parasites of livestock there are examples of species whose transmissibility is known to be affected by climate. The larvae of *Haemonchus contortus*, a gastro-intestinal parasite of sheep, require mean temperatures $>18^{\circ}\text{C}$ for normal development, whereas the development of *Ostertagia circumcincta* larvae is suppressed above 15.5°C . As both require moisture, the former is an organism of summer rainfall areas, and the latter of winter rainfall areas (Southcott *et al.* 1976).

There is less known about the parasites of Australian native vertebrates, and most of the published investigations have been taxonomic (e.g. Beveridge & Durette-Desset 1992). Arundel *et al.* (1990) undertook one of the few epidemiological studies, which demonstrated that helminth parasites can cause considerable mortality in Eastern Grey Kangaroos, and concluded that development of free-living larvae is influenced by climate. In North America, the Moose *Alces alces* can exist sympatrically with White-tailed Deer *Odocoileus virginianus* only in those areas where circumstances do not favour persistence of infective larvae of the meningeal worm *Parelaphostrongylus tenuis* (Gilbert 1992). Hence, climate change may indirectly influence the distributions of terrestrial vertebrates through its effect on the probability of disease transmission.

Mechanisms for coping with climate change

Passingham (1993) recognised that there are three means by which a species might survive climate change: range change to track shifting climate zones, tolerance of the change, and/or microevolutionary change. Examples are presented which demonstrate that tolerance in the form of behavioural plasticity may counter climate change, but tracking appears implausible for many small terrestrial species.

Tolerance

The Red Fox (*Vulpes vulpes*) has a complex social structure which can be modified to cope with environmental change. Zabel & Taggart (1989) have demonstrated an effect by the *El Niño* phenomenon on the food supply of a population of foxes on Round Island, Alaska. Increased water temperatures in the Bering Sea were associated with widespread nesting failure in the seabird species which comprise most of the summer diet of the foxes. Resorption and preimplantation loss are known to occur in pregnant vixens (Ryan 1976), a common cause of which is nutritional stress (see Moustgaard 1969). Hence, if the available food was uniformly distributed amongst the foxes, total reproductive failure in the fox population

may well have occurred. However, on Round Island, dietary changes in smaller, less common, and less accessible seabird species were associated with changes in the social structure of the foxes. Polygyny, the reproductive mode prior to the dietary change, was supplanted by monogamy. The male's help is essential for capturing and delivering prey to a lactating female and her litter (Kleiman 1977); thus the change in the social structure meant that assistance provided by the male fox was focussed on fewer cubs at a time when it would have been more difficult for the males to procure food. Individual reproductive success (in terms of cubs reared to sexual maturity) of the reduced number of breeding females was not significantly affected by the *El Niño* phenomenon. Hence, a (temporary) climate change which lead to total reproductive failure of the two seabird species most prominent in the diet of the foxes did not in turn lead to total reproductive failure in the foxes.

The Eastern Long-necked tortoise (*Chelodina longicollis*) has simpler behavioural patterns than the Red Fox, but still has some plasticity. It appears to adjust its selection of nesting sites to take account of meteorological parameters likely to affect incubation temperature. At Armidale, New South Wales, the species digs nesting chambers in unshaded areas, which increases insolation and hence egg temperature, and shortens incubation (Parmenter 1976). The same species at Roseworthy, South Australia, digs about two-thirds of its nests in sites shaded for more than half of the day (Stolt 1987, 1988). Nest temperatures were not recorded at either site, but mean daily temperatures during the incubation period are higher at Roseworthy (3.9°C higher in January) and cloud cover is less frequent (0.7 oktas less in January). Thompson (1988b) has demonstrated that unshaded nests of *Emydura macquarii* at Barmera, South Australia can be 2.6°C warmer than shaded nests, and attributed deaths in some unshaded nests to excessive heat. Thus it is reasonable to speculate that *C. longicollis*, like the species of testudines considered by Bull *et al.* (1982) and Schwarzkopf & Brooks (1987), positions its nests relative to shade to obtain optimum subsurface temperatures for incubation.

Tracking

Durale *et al.* (1992) dated late Holocene vegetation changes at two sites in Iowa which correspond to a rate of retreat of prairie of 300–600m per annum. However, the anticipated rate of anthropogenic climate change is much greater than in the past (Possingham 1993). With the low relief of the inland plains of northern South Australia, mean thermal gradients are slight, and a typical distance between isotherms corresponding to the predicted annual rate of temperature change of 0.03°C is 2000 m. Because many bird species of the Australian arid zone are

nomadic (Wiens 1991), tracking climate change is physically and behaviourally possible. However, sedentary species may have behavioural difficulties. Few data are available on the dispersal capability of small terrestrial vertebrates, but the longest dispersal movement recorded by James (1991c) for any individual of five species of *Ctenopus* was 605m, indicating that unassisted dispersal is most unlikely to be able to track climate change at the predicted rate.

Possingham (1993) points out that comparisons of dispersal capability with the rate of climate change may be simplistic. The comparison is useful to identify species which are physically incapable of tracking climate, but cannot by itself determine competence. There must be subsequent stages in the process of identifying species at risk, such as consideration of physical barriers and inter-relationships between species. Even if *Ctenopus* spp. were physically capable of tracking climate change, there is a close and presumably obligatory association between many species of *Ctenopus* and *Triodia* and *Plectrocline* spp. (spinifex grasses) and their attendant termites. These are primarily distributed in infertile, sandy soils (Graetz *et al.* 1988), which indicates that spinifex-dependent species of *Ctenopus* which are less tolerant of increased temperatures would be unable to track climate change across changes in soil fertility and type. For vertebrates in the north of South Australia, tracking temperature changes means a generally southern extension in range (with or without a northern contraction; a separate issue which would depend on the upper limits of tolerance), but for *C. pantherinus* there would be constraints because long distance dispersal or even local spread of *Triodia* and *Plectrocline* seem to require considerable time (Jacobs 1982). Also, these grasses would not extend into heavy clay soils and limestone plains, the latter being generally south of the present distribution of *C. pantherinus*.

The steepness of climatic gradients in mountainous areas is much greater than on plains, and thus altitudinal tracking of climate change is much more feasible than latitudinal tracking for small terrestrial vertebrates. Generally, a short climb in altitude corresponds to a major shift in latitude (Peters & Darling 1985). Over a distance of about 15 km in the Adelaide Hills, a 500m increase in altitude is associated with a fall in January mean maximum temperature of about 5°C, and a rise in mean annual rainfall of about 600 mm. However, whilst the climate as one component of a species' environment may track up a mountain, other components of the environment may be fixed; for example, substrate structure and fertility usually change with altitude.

To allow tracking requires the linking of areas managed primarily for conservation along latitudinal and altitudinal gradients (Norton 1990). The review

of nature reserves in south-eastern New South Wales undertaken by Margules & Stein (1989) confirmed that a single, long, narrow, rectangular reserve aligned along an altitudinal gradient would be the configuration which would most parsimoniously meet the dominant environmental requirements of temperature, rainfall, and substrate for 26 canopy tree species which occur in the region. Mackey *et al.* (1988) note the necessity and argue the validity of using vegetation data as surrogates for data on fauna habitat in the present circumstances of paucity of the preferred primary data, and advocate a focus on ecological gradients in order to provide a margin of safety in assessing areas for conservation value. However, because of the low relief of much of South Australia, only latitudinal gradients are possible in most areas.

Conclusion

The paper has focused on a number of studies which have relevance to the issue of climate change. On reviewing the topic, it is apparent that the zoological base from which changes may be predicted is imperfect. Reliable information on the present distribution, abundance, population dynamics, and

interspecific relationships of Australian vertebrates is limited (Norton 1990), but there is sufficient information to indicate that climatic influences on the distribution of many animals operate through mechanisms which are subtle and as yet poorly understood, and sufficient information to warrant a conclusion that climate change of any magnitude is quite likely to affect the distributions of many species of terrestrial vertebrates.

Conclusions about the fate of individual species are at present speculative. Deterministic studies such as those undertaken on kangaroo populations are less speculative than mechanistic studies because of the complexity of the means by which climate influences the biota, but mechanistic examinations are complementary in that they may reveal critical aspects of detail not apparent to deterministic considerations.

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SOME POSSIBLE EFFECTS OF CLIMATE CHANGE ON VEGETATION

*By ROBERT BOARDMAN**

Summary

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One of the most difficult tasks for managers of land which grows long-lived plant species, (species that dominate ecosystems), is how to assess that change in environmental conditions is actually of significance to the present ecosystems, and what to do to ensure that the ecosystem, rather than the species themselves can be maintained. Practical things to do which will make adaptation possible are limited by the indefinite nature of time frames. Areas of the State north of Kangaroo Island extending to the northern State boundary, are the parts most sensitive to changes in vegetation. It is likely that the most strongly threatened species in the long-term are the perennial species which dominate woodland formations. Low sclerophyll woodland and mallee formations appear to be particularly at risk.

Key Words: arid zone, vegetation, climate change impact, Goyder's line, Eucalyptus.

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KEY WORDS: arid zone, vegetation, climate change impact, Goyder's line, *Eucalyptus*.

Introduction

South Australian vegetation is strongly associated with climates which are dominated by cool wet winters and warm to hot dry summers. Rainfall and potential evapotranspiration occur at levels which impart a range from sub-humid to arid climate types. The vegetation has been classified by its form (Specht 1975; Boonisma & Lewis, 1976; Atlas of South Australia 1986). These forms show marked correlation with isohyets and lines of equal potential evaporation.

A large proportion of species in the semi-arid and arid zones are trees and shrubs which are classed as "sensitive" by dendroclimatologists and dendrochronologists (Fritts 1976). Tree rings represent the end point of the long-lived perennial plant's allocation of carbohydrate resources produced by photosynthesis. This link emphasises the reliance of semi-arid and arid zone vegetation on a tolerable infrequency of favourable growing seasons when conditions enable species to maintain their place in ecosystems of the region.

Climate change scenarios for the Australian region (Climate Impact Group 1992) are now less definite than the original single emissions scenario (IPCC 1990) from which some of us worked in 1988 (Greenwood & Boardman 1989; Boardman 1989). Global warming models are less simplistic and now include a range of gases, responses in cloudiness, absorption of heat by the oceans and a degree of climate "sensitivity", not included previously. The CSIRO GCM model has provided plausible ranges of local temperature warming and changes in rainfall per degree of global warming overall.

Sub-regions have been added in the rainfall change scenarios which, so far as S.A. vegetation is concerned, largely reflect earlier findings. Areas of the State north of Kangaroo Island are placed in sub-region A by Climate Change Group (1992) and this extends most of the way to the northern boundary. The reduction in winter rain, despite a trend towards a greater proportion of annual rainfall in summer together with a marked rise in potential evapotranspiration has been modelled, and leads to greater droughtiness and diminution of growing season described for this part of the State (Appendix 1) (Boardman 1989, 1992).

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Areas of the State south of Fleurieu Peninsula are placed in sub-region B: this is a sub-region unlikely to suffer marked change in gross rainfall and may not even see a decrease in winter rainfall. This fits in with earlier prognoses already deduced for this part of the State. Impacts on vegetation seem likely to be minimal and possibly will see a more favourable set of growing conditions. Dendrometrical data on native forest in the Lower South-east (Ruiter 1964) indicate that the native tree species are better adapted to a summer rainfall climate than the Mediterranean type which has persisted since the last glacial epochs. That is, most of their evolutionary adaptation took place in a climate similar to that now present in the eastern part of NSW (Boardman 1986).

The impact of ENSO (El Niño — Southern Oscillation) has not been included in GCM models. This appears only to affect sub-region A of the State which is bisected by it (Allen 1988). The boundary between ENSO affected areas and those dominated by the Antarctic polar circulation systems lies along a NW-SE direction which crosses the northern Flinders Ranges. The "settled areas" of the State SW of the boundary zone are not directly affected by ENSO, and only indirectly influenced by the alternate system, called La Nina.

It is the time-scale of changes rather than their degree which is different, compared with the early model, and it has been extended. A range of temperature change is now given rather than an average. However, the median temperature change for the 2070 scenarios is similar to that used in 1988, and these will be used specifically here. Physiological processes of plants and microflora are more sensitive to temperature than ecological processes, but this sensitivity to temperature change will be observed through the symptoms which will be ecological in nature and reflect the impacts through interactions within and between species. They will be the first changes to attract attention. We expect to find features which can be measured and which will indicate the nature of changes taking place.

What is the nature of changes that may be expected?

The sequence of reviews adopted by the organisers of this meeting implies that the most obvious effects of climate change indicated for South Australia will be noticed in soils (which I think is unlikely) and in areas we recognise as wetlands; namely, low coastlines and coastal swamps, swales between sand-dunes, lakes and lunettes. Most indications of the impact of seasonal changes in rainfall distribution, both in quantity and intensity, and a warmer climate indicate that it will be topographically low-lying areas which will be affected early during the process of change. It seems reasonable to suggest that it will be the vegetation in areas most

sensitive to direct and intense climate change which shows the visible signs first, rather than the animals and the soils. However, it may be tempting to suggest that it will be the microflora and microfauna which will be most sensitive to climate change until it is realised that both are more closely linked to the dominant higher-plant species of an ecosystem and the weather, than to climate (Howard 1967; Lewin, 1985; Simpson 1967).

It appears likely that the first visual changes to vegetation will result from changes in physiological processes that are mediated through plant metabolism. In this respect, the tallest elements in ecosystems, especially trees, are likely to show the effects first. Trees are more likely to suffer climate change effects than shrubs, the result of their ability to produce a bole, or trunk. As the bole lengthens and its diameter becomes larger, a greater amount of tissue needs sustenance which is unnecessary for lesser plants. A sheath of new tissue is added each growing season comprising extra phloem, or bast, bark and meristem tissue, the cambium. It is a cost for keeping the tree in a lofty position in the ecosystem. There is no difficulty with maintaining this structure in a stable climate; allocation of resources is attuned to the situation; wood growth is laid down in a predictable fashion including well into old age. Waring (1988) and Franklin *et al.* (1988) have discussed the nature of changes which may result in tree death. There is a complex series of alternate pathways which lead to a single result. The first of these is a reduction in food substance available for new wood production.

Different environmental stresses affect the major components of the resource-budget allocation. There is a hierarchy for normal allocation of carbohydrate within a tree. Stem growth only occurs once the resource demands of new leaves, new roots and an intrinsically-regulated reserve allocation into storage ("recovery insurance") has been accommodated. Hence, the time when physiological state is most suitable for assessment is just before a flush in new leaves becomes apparent. Flowers are not produced annually and when they do depends on the amount of stored resources accumulated. At this time carbohydrate and nutrient reserves in twigs, older foliage, large diameter roots and the stem itself are at their greatest. The arbiter of this is the amount of new wood produced per unit of foliage.

Fritts (1976) has produced model diagrams which illustrate the factors which interact and lead to formation of a narrow growth ring in the trunk. His model has two parts which can be related to the S.A. situation, currently and as it may develop over the next century. Part A of his model contains relationships associated with low precipitation and high temperature *during the growing season* that lead to the formation of a narrow ring in trees on dry sites. Part B is a

possible precursory extension to part A, times when low precipitation and high temperature occur *prior to the growing season* and add to the amount of stress. The complexity of these reactions is indicated by the two parts which each have 24 possible stages. When both parts meet they act additively and directly on the cambium, but only combine for the last three stages. Combination of parts A and B is not an uncommon situation in S.A. when dry winter precedes a droughty growing season. The net result is reduced rates of cell division in the cambium and so fewer wood cells become differentiated, as a consequence of low production of growth regulatory substances (plant hormones) and food resource. Several other common factors affect the cambium when a narrow ring is formed including years of intense flower and seed production (mast years) and attack by pests, mainly defoliators but also including bark beetles and sawwood borers. Dendrochronologists have attempted to identify the range of causes when a narrow ring is formed and some models exist for these situations (Fritts 1976).

Palaeoecological plant studies have shown cycles of change have already been experienced by the genera and species still present in Australia. Species may be adapted to the scenario in different ways or may be tolerant in different degrees. A sustained trend away from normality will have an effect proportional to any dormant evolutionary adaptation already incorporated into the genes. We have no ready way of knowing what these might be in specific cases. This position is aggravated by the apparent lag of many centuries before consequent vegetation changes occurred in the past. The current climate change scenarios preclude this significant lag period apparent in the past. If a trend in the rate of change in climate becomes apparent then the stress impacts are likely to accumulate in ways not seen before. The impact is then likely to be similar to one of a range of possible impacts such as illustrated by Barker (1989) looking at different recurrent periods between fires in *Acacia* woodland.

Periods of extended drought are not particularly harmful if trees have well-established root systems and foliage canopies, partly because drought is reckoned in relative terms to the normal climate. Where there has been natural selection by drought, trees rarely die from drought. In the short term, adaptation may help retain reserves by temporary reduced demand. Trees, such as those in S.A. are probably more acclimatised to chronic drought than most high forest tree species. They already have features which reduce the impact of drought: low leaf area indices (leaf area per unit of ground area), smaller, thicker leaves, strap-like petioles leading to panphotometric (drooping) leaf posture; leaf oils and wax coating. Some species readily drop older foliage to reduce leaf area. The adjustments can mean that wood production is comparable with that on more mellow sites because

respiration load is less. A considerable vegetation inertia occurs with existing, mature tree-dominated ecosystems because trees influence microclimate so significantly, especially in the availability of sunlight and top-soil moisture. They can also alter the character of soil chemistry as they store and retranslocate scarce nutrients in tissues away from recycling.

Consideration of microclimates emphasises that the regeneration phase, when seedlings become established, is possibly the most critical phase in the life-cycle of higher plants. The game is one of numbers and of resource reserves in the seed. Most species in S.A. have adapted so that they produce large numbers of seeds with small or negligible food reserves, so regeneration becomes a matter of numbers. Vegetational change associated with climate change will depend therefore, on the reproductive vigour of invasive and endemic species and whether microclimates and provision of soil conditions are equally-suited to the potential invader.

Persistent drought, however, halts photosynthesis, leads to depletion of carbohydrate reserves, and depletion of defensive compounds. Individual species within a plant community will vary in the rate of reaction. Air turbulence and wind shear, especially of strong, hot, dry winds, as well as chilling winds, will aggravate drought and damage foliage; taller trees are more at risk than short ones. Shallow-rooted trees growing over stony materials allocate more resources to root growth than to shoots. Even so, they are susceptible to infrequent intense drought and are liable to die off in whole groups. Drought will inhibit microbial activity and reduce mineralisation of nutrients from litter; higher temperatures in times of rain will accelerate mineralisation rates but also accelerate leaching losses — both conditions in a changed climate will limit the quantity of nutrients available. Nearly any stress, if it becomes sustained, leads to forest and woodland decline; it reduces leafy canopy, photosynthetic activity, stored reserves and defensive factors throughout trees more so than in lesser vegetation. Consequently the balance between species and individuals will alter and, in ecological terms, a seral change will be initiated.

Scientific investigations since 1988 into impacts of factors in the climate change situation on vegetation mainly have been concentrated upon the effect of elevated atmospheric carbon dioxide concentrations on physiological and metabolic processes. This has been discussed frequently as a "fertilizer effect" and evidence in the field as well as numerous laboratory studies have been made to adduce its impact. The subject was reviewed in Australia by the Ecological Society and Society of Plant Physiologists (1992, 1993; Gifford 1993).

The impact on biodiversity has been given much less attention. It has been reviewed by Possingham (1993)

at the species level in terrestrial ecosystems. He took a mechanistic approach to an implied rapidly-changing physical environment and concluded that, in the short-term, extinctions will occur through direct interactions of species with changes in the climate of their environment. A second set of species face extinction either because of opportunities available to disease-causing species or to loss of mutual support (eg. loss of shade) or unsustainable symbiotic relationships. Particular "keystone" species in the association may become extinct and so change the essence of that system. Direct inter-specific competition is considered to be the least likely cause of species loss from a present-day community. Possingham (1993) argues that each species will be affected by one, or any combination of four basic pathways; change in geographical position to follow favourable climatically-controlled features of the current range; selection of tolerance to climate change within the current zonation; micro-evolutionary change, and extinction. He suggests that it should be possible to use autecological information to help track the pathways to new synecological combinations of species. This supports the idea that there is a need and an opportunity to identify "indicator species" and particular features of these for measurement.

South Australian vegetation in the late 20th Century

The foregoing discussion has described general trends and effects. Once one wishes to review the local situation, one has to observe its irregularities. The Flinders Ranges, for example, cause the southern climate patterns to extend northwards but any change is modified by a reduction in maritime conditions (Boardman 1992). This is reflected, for example, in the direction taken by Goyder's Line between Eudunda and Crystal Brook. When climate change is considered, however, it has to be noted that rainfall, temperatures and particularly maritime conditions are modified by the topographically-high region.

Natural vegetation in rural South Australia has been affected at low altitudes by the direct influence of changes in sea levels associated with Pleistocene glaciation. A significant part has been affected by marked climate changes associated with the Ice Ages. Collectively there have been both edaphic and geographic barriers to plant migration. Both of these barriers have meant that a considerable, but unknowable, number of native species has the capacity to grow in S.A., to colonise sites and compete strongly with local species, but these have been unable to reach it by natural means. On the other hand, the species which are present have suffered genetic depletion through intense environmental selection pressures in the last two million years in their refugia, and have

limited intrinsic adaptability to change in directions not already encountered (Boardman 1986).

Much of the vegetation outside the settled areas and influenced by Aboriginal peoples, can be classed as ancient secondary vegetation. A large proportion of the remnant vegetation, including conservation reserves in the settled areas should be regarded as modern secondary or tertiary vegetation (Barker 1989; Boardman 1986). These last two categories were first affected by European migration purposefully, and secondly, but without direction, from escapes of introduced domestic animals and plants which have become feral. Klotz (1983, 1985, 1987) has assessed plant introductions in great detail and has identified these from plant migrants and some native species. Klotz (1987) also evinced evidence that intense hunting, especially on isolated land, like Kangaroo Island, very early in the period of settlement by migrants, decimated native grazing species of kangaroo and wallaby, transforming the native plant ecosystems rapidly and dramatically. Fire frequency and species life-span interact and this affects the stability or vulnerability of ecosystems (Barker 1989). Such information is used to manage range in the pastoral zone. Frequent devastating fires in the first half of this century, as the population increased, and fire protection measures in the latter half, also have had a strong visible impact on partially cleared and uncleared native ecosystems in the areas south of the 32nd Parallel (Grandison 1983).

The studies of Klotz (1987) are a reminder that weeds are likely to be the bane of any attempt by native species at colonisation of new habitat, even if the habitat is an amenable one. Many of the weed species introduced from overseas are much more adaptable (notice Klotz's method of separating natural migration from garden escape) and often they have a much more aggressive behaviour. Many are natural pioneer species. Two examples of weed species likely to be affected in the climate change scenario and able to migrate southwards and compete with native species needing to do the same to survive, are Montpellier broom (*Genista monspessulana*) and Salvation Jane (*Echium plantaginifolium*).

It is likely that the most strongly threatened species in the long-term are the perennial species which dominate woodland formations. Low sclerophyll woodland and mallee formations appear to be particularly at risk. These formations occur in the zone with an average growing season, in the best possible conditions, of from 3.5 to 5.5 months. It is changes in the distribution and remains of the physically-dominant species in ecosystems which have signalled past climate changes, whether it is through different levels of pollen deposits, whose abundance speaks for itself, or through macro-fossils. On the other hand, many of the perennial herb and low shrub layer species

in local ecosystems are more ubiquitous than the ecosystem-dominants, and frequently less constrained by particular site factors. This is partly because of similarity in the microclimates they generate, and partly, because tree-dominated ecosystems provide amelioration of the weather from shelter and shade. The huge demand for moisture by trees in local ecosystems means that tolerance of chronic drought by understorey species is normal. This is the case when the understorey of the mallee woodlands is compared with that of forest ecosystems in the Mt Lofty Ranges showing that many species have a continuity in distribution across a wide range in rainfall from near 250 mm in the Murray Mallee to around 1000 mm at Cleland Conservation Park (McCann 1989; Dashurst & Jessop 1990).

Investigations of woodland productivity in the S.A. semi-arid zone in relation to climate

Trees, as long-lived perennial plant species, frequently dominate all or major parts of the ecosystems that contain them. They accumulate a major part of ecosystem solid dry matter in their wood and bark tissues. Wood and bark are that part of the perennial plants which sequester CO_2 and which helps to maintain stability of this gas in the atmosphere. The Research Branch of the former Woods and Forests Department has investigated the amounts and trends in wood accumulation by trees growing in stands. It has been recorded on an unit area basis, either as volume per hectare (preferred by foresters because it is bulkiness which is of interest) or as dry weight per hectare. The overall effect over a long time determines productivity.

Studies in S.A. were stimulated by apprehension about fossil fuel supplies, future costs of fuel, and the need to assess renewable fuel resources in the mid-70's (Kiddle *et al.* 1985). This work was expanded upon when the Electricity Trust of South Australia (ETSA) wished to assess the opportunity to sequester CO_2 produced from their power stations (Boardman *et al.* 1992). Productivity of twenty tree species growing in plantations over a range of sites, soils and climate, has been measured, mostly as single species, but also as mixtures of species. About one-third have been remeasured which means we have been able to establish trends with increasing age. The use of plantations is useful as both the age and the density of trees in the stand, or level of occupancy of site are known factors. It also means that we were able to extend methods from existing forestry science and use them to extrapolate findings over time and space, to other localities. We have compared our results with general models of forest productivity, to see how local stands compare with their counterparts on a global-scale.

World plant life-zone classification (Holdridge 1974)

indicates that sustainable tree-dominated ecosystems are unlikely to exist on land in S.A. receiving less than 250 mm rainfall. Consequently our research set out to include all well-established plantations in a zone with average rainfall between 250 mm and 600 mm. In the event, none of the plantations suitable for the study were found in areas which received rainfall of less than 340 mm. Dryland cereal cropping, which requires 220 mm of winter season rainfall to produce an economic crop of 6bu/acre [540L/ha], rarely extends below the 280 mm isohyet (French 1989). However, ETSA asked that potential for tree-growing in the 200 – 300 mm rainfall zone should be given special consideration. What we found is of interest in the present context.

At an ecosystem level, soil moisture replenishment and capacity to store water are critical factors which determine whether trees will grow or not. In S.A. there is a surprisingly frequent inverse correlation which exists between soil depth and fertility; a large number of shallow soils, which have low capacity to store moisture and physically restrict root development, are fertile and an even larger proportion of deep soils, able to absorb all the rainfall reaching the ground and provide unrestricted physical capacity for root development, are infertile in the topsoil where 85% or more of roots are normally found. In both cases productivity is markedly below the level expected when conditions are the best that can be expected.

Mallee woodland gives way to tall shrubland with *Acacia* species within the 200–300 mm rainfall zone. There are exceptions and an hiatus is present as in western Eyre Peninsula, where it is associated soils conditions that are unsuited to either life-formation. Average rainfall is a poor delimiting factor because it is the critical periods and intensity of rainfall which count the most. The annual rainfall in drought years is often as little as half that of median years. In this zone, also, infrequent long periods of drought persist. These considerations have led to the concept and definition of "influential rainfall". The quantity of moisture available to prevent wilting, expressed as its equivalent in rainfall, is 100 mm and it has to be present in the upper root zone. The factors which determine influential rainfall have been assessed for dryland cereal cropping and sites with natural vegetation, potentially suitable for cereals. Influential rain, on average is needed for 3–4.5 months in 12. The minimum amount of influential rainfall to produce 2.0 dry t/ha/y of wood exceeds 200 mm. That is to say, in this zone sites capable of producing wood have to receive water in excess of that received from natural rainfall directly. In other words, they have to be "run-in" sites which receive water as run-off or percolated as drainage from areas of higher elevation. The minimum amount of the total water which has to be available is found to be the equivalent of 300 mm. In months when there is a fall

of rain sufficient to promote growth (ie. a surplus over respiratory needs), it needs to be supplemented by at least 25%. Seasonal variation is critical for vegetation survival in this zone. The frequency distribution of sustained lengths of rainy season for a number of representative weather stations has been investigated and is summarised in Table 1 (Boardman 1980). It emphasises that growth rings in trees may not be an annual sequence of rings but of adequate rain events.

TABLE 1. The frequency per century of rain periods of a given duration for sites in the 200 mm to 300 mm average rainfall zone of South Australia.

Average rainfall	300 mm	250 mm	200 mm
Rainy season duration:			
At least 5 months	17 years	5 years	1 year
At least 4 months	40 years	17 years	5 years
At least 3 months	70 years	35 years	16 years
At least 2 months	90 years	63 years	33 years
At least 1 month	96 years	85 years	65 years

Trumble (1937, 1939), considering dryland cereals requirements, showed that 200 mm gross annual rainfall will provide annual herbaceous vegetation with wilt-free conditions for up to 3.6 months. Trees in woodland, however, intercept a proportion of the gross rainfall with their leafy canopies. If the trees are mature and spaced so as to absorb all the capacity which is available for them to lay down new wood, ie. the site is fully occupied by the smallest number of trees able to do so, then throughfall, rain able to wet the soil, is reduced to 160 mm. This effective accession will only provide for 1½ months growing season, which is quite insufficient to support woodland. At 300 mm rainfall, the throughfall is likely to be sufficient for 4.5 months. An actual growing season of four months, the minimum likely to carry a sustainable stand of woodland, calls for a gross rainfall equivalent of 320 mm in Upper Eyre Peninsula and for 310 mm in the Murray Mallee. Following Trumble's argument, the "run-on" requirement from these considerations is for about 150 mm water, but it must be delivered in the Winter rainfall season to be "influential".

Alternative approaches to the question of minimum water requirement for a woodland without "gaps" has been provided by Specht (1973, 1975, 1983) and Walker *et al.* (1986, 1988). Both have dealt with natural vegetation of the kind being discussed here. Specht worked from the direction of evaporative demand and defined the tolerable limits to evapotranspiration stress. Evergreen, perennial plant communities, under conditions which are the best to be expected, need a minimum net monthly supply of soil moisture determined by rain that falls and any accession or loss of water in the soil. He called this the "soil available

water" requirement and it ranges from 37.5 to 62.5 mm. Sites able to sustain woodland are characterised by a need for additional water which is equivalent to 27% of average rainfall for the month. In turn, this implies that there is adequate storage available in the soil within reach of roots. Taking canopy interception into consideration indicates that run-on component needs to be not less than 47% of rainfall at a 200 mm site, again showing that about 300 mm of rainfall equivalent is needed to sustain woodland formations.

The stand structure of woodland which will optimise net dry matter production from the site factors available can be deduced from the research of Specht and Walker. Specht has found strong relationships between the foliage projected area (FPC) of the tallest plant structural layer (overwood - FPCo), and of the whole ecosystem (FPCt), to his evapotranspiration coefficient, and based his findings on a very wide sample of mature Australian native ecosystems. Mature low woodland in the 200-300 mm rainfall zone has an overwood cover of 32 to 42% and total ecosystem foliage cover of 75±6%; ie. there will be about 20% bare ground. Walker's group took a different view of foliage cover which recognised its fragmentary structure corresponding to about 80% of FPCo. The optimum cover based on their work, and adjusted to FPCo terms, suggests that cover of 32±5% should be adequate to sustain low woodland on run-on sites in the 200-300 mm rainfall zone of S.A. Their models allow one to assess stocking rates in young-age and juvenile stands as well as mature ones.

Thus, the effectiveness of water supply can be associated with net primary production and the length of the growing season. These have both been mapped by for present-day climate and the median scenarios by Greenwood & Boardman, (1989) and Boardman, (1992). Net primary production is likely to change by 18% for each incremental gain or loss of 10 mm in average annual rainfall. These preliminary findings, now likely to be extended further ahead in time, are sufficient to indicate the level of changes which can be expected and where the changes are more likely to occur. The maps show the "best that can be expected" and until the sub-optimal standing of existing vegetation can be assessed, they form a working basis for taking adaptive action. Table 2 lists the tree and shrub species whose survival and distribution in the zones most sensitive to change, are the ones likely to be influenced by threats and opportunities presented by the climate change scenario. This is based on Chippendale & Wolf (1981); Boomsma (1981), Boomsma & Lewis (1976) and Costermans (1983). Table 3 shows the eucalypt species sorted into their botanical affinities (Pryor & Johnston, 1971) in relation to changes in ecological status that are possible.

TABLE 2. Tree and shrub species whose status is likely to be significantly affected by climate change scenarios for South Australia. Note, ecosystems affected occur principally in sub-region A (Climate Impact Group, 1992).

Species	Common Name	Eucalyptus Groups, Pryor & Johnston Class'n	POTENTIAL CHANGE IN STATUS WITH CLIMATE CHANGE SCENARIOS			
			Major reduction in distribution	Some site loss frequent	Gain or loss not clear	Major gain in colonisation
<i>Acacia reinodes</i>	Wirilda		✓			
<i>Callitris canescens</i>	Grey cypress pine		✓			
<i>Casuarina stricta</i>	She oak		✓			
<i>Cardonocarpus cotinifolius</i>	Native poplar		✓			
<i>Eucalyptus anceps</i>	White mallee		✓			
<i>Eucalyptus angulosa</i>		SLE:IB	✓			
<i>Eucalyptus brachycalyx</i>	Gilja	SLOAC	✓			
<i>Eucalyptus cladocalyx</i>	Sugar gum	SLE:IB	✓			
<i>Eucalyptus conglomerata</i>	Cong mallee	SIS:A	✓			
<i>Eucalyptus gonilocalyx</i>	Long-leaved box	SLE:IA	✓			
<i>Eucalyptus gracilis</i>	Yorrell	SPIFB	✓			
<i>Eucalyptus lansdowneana</i> ssp <i>lansdowneana</i>		SIX:A	✓			
<i>E. lansdowneana</i>	Crimson mallee		✓			
<i>E. lansdowneana</i> ssp <i>albopurpurea</i>	Pt. Lincoln mallee	SUNEAA	✓			
<i>E. largiflorens</i>	River box	SUNEAB	✓			
<i>Eucalyptus leucosylon</i> , ssp <i>leucosylon</i>	S.A. blue gum	SUDEC	✓			
<i>Eucalyptus remota</i>	Mallee ash	SUX:CE	✓			
<i>Eucalyptus rubida</i>	Candlebark gum	MAKEB	✓			
<i>Eucalyptus rugosa</i>	Kingscote mallee	SPINF	✓			
<i>Eucalyptus microcarpa</i>	Grey box	SLE:A	✓			
<i>Eucalyptus odorata</i> , var. <i>odorata</i>	Peppermint box	SUC:DB	✓			
<i>Eucalyptus pauciflora</i> , ssp <i>pauciflora</i>	Snow gum	SUNEBA	✓			
<i>Exocarpus cupressiformis</i>	Native cherry	MAKHAA	✓			
<i>Hibbertia aspera</i>	Guinea flower		✓			
<i>Spyridium vexilliferum</i>	Winged spyridium		✓			
<i>Acacia victoriae</i>	Elegant wattle		✓			
<i>Alogyne huegelii</i>	Lilac hibiscus		✓			
<i>Bursaria spinosa</i>	Bursaria		✓			
<i>Callitris verrucosa</i>	Warty cypress pine		✓			
<i>Correa reflexa</i>	Common Correa		✓			
<i>Eucalyptus albens</i>	White box	SUL:G	✓			
<i>Eucalyptus calycogona</i>	Square-fruited mallee	SIX:D	✓			
<i>Eucalyptus foecunda</i>	Slender-leaved mallee	SIZ:B	✓			
<i>Eucalyptus incrassata</i>	Ridge-fruited mallee	SLOAB	✓			
<i>E. macrohyncha</i> , ssp <i>macrohyncha</i>	Red stringybark	MAHACA	✓			
<i>Eucalyptus oleosa</i>	Glossy red mallee	SIT:C	✓			
<i>Eucalyptus poroxa</i>	Mallee box	SUNCC	✓			
<i>Eucalyptus socialis</i>	Red mallees	SIT:L	✓			
<i>Metaleuca lanceolata</i>	Mooreah		✓			
<i>Metaleuca uncinata</i>	Broombush		✓			
<i>Santalum</i> spp. except <i>S. murrayanum</i>	Sandalwood; Plum bush; Quandong		✓			
<i>Templetonia exera</i>	Round templetonia		✓			

TABLE 2 Cont.

<i>Templetonia retusa</i>	Parrot bush		
<i>Acacia papuocarpa</i>	Western myall		
<i>Callitris preissii</i>	Southern cypress pine		
<i>Cardonocarpus pyramidalis</i>	Bell fruit		
<i>Dodonaea</i> spp.	Hopbushes		
<i>Eremocitrus glauca</i>	Desert Lime		
<i>Eucalyptus behriana</i>	Broad-leaved box		
<i>Eucalyptus calcaranea</i>	White mallee	SUDGA	
<i>Eucalyptus cyanophylla</i>	Murraylands mallee	SLE:GC	
<i>Eucalyptus diversifolia</i>	Coastal white mallee	SLE:H	
<i>Eucalyptus flindersii</i>	Grey mallee	MABAC	
<i>Eucalyptus intertexta</i>	Gum-bark coolibah	SNEEK	
<i>Eucalyptus petiolaris</i>	Eyre-Pa. blue gum	SUH:A	
<i>Eucalyptus ptilata</i>	Silver mallee	SUX:CE	
<i>Eucalyptus leucocylon</i> , ssp. <i>pruinosa</i>	Inland blue gum	SLE:GB	
<i>Eucalyptus trivalvis</i>	Victoria Spring mallee	SUX:CC	
<i>Eucalyptus viridis</i>	Green mallee	SIF:E	
<i>Geijera parviflora</i>	Candle bush	SUNEHA	
<i>Acacia aneura</i>	Mulga		
<i>Acacia brachystachya</i>	Umbrella mulga		
<i>Acacia linophylla</i>	Sandhill mulga		
<i>Acacia oswaldi</i>	Oswald's wattle		
<i>Acacia salicina</i>	Broughton Willow wattle		
<i>Acacia stenophylla</i>	River cooba		
<i>Acacia tetragonophylla</i>	Dead-finish		
<i>Callitris columnaris</i>	Northern cypress pine		
<i>Casuarina cristata</i>	Belah		
<i>Cassia</i> spp.	Silver-; Sturt cassia		
<i>Eremophila</i> spp.	Emu bushes		
<i>Eriostemon angustifolium</i>	Waxflower		
<i>Eriostemon linearis</i>	Waxflower		
<i>Eucalyptus concinna</i>	Victoria Desert mallee	SLE:I	
<i>Eucalyptus odorata</i> , var. <i>angustifolia</i>	Peppermint box	SUNEBB	
<i>Eucalyptus straticolux</i>	Kopi mallee	SLE:F	
<i>Eucalyptus yalaensis</i>	Yalata mallee	SIT:M	
<i>Eucalyptus yumbarrana</i>	Yumbara mallee	SIT:OA	
<i>Exocarpus aphyllus</i>	Jointed native cherry		
<i>Myoporum platycarpum</i>	Sugarwood		
<i>Nitraria billardiera</i>	Nitre bush		
<i>Chenopodia</i> spp.	Saltbushes		
<i>Mairiana</i> spp.			
<i>Rhagodia</i> spp.			
<i>Pinusporum phillyreoides</i>	Weeping pittosporum		
<i>Sida petrophila</i>	Rock sida		
<i>Grevillea nematophylla</i>	Silver-leaf water bush		
<i>Grevillea striata</i>	Beefwood		
<i>Hakea leucopiera</i>	Needlewood		
<i>Homodendrum oleaeifolium</i>	Bullock bush		

TABLE 3. Eucalyptus species potentially affected by climate change scenarios in sub-region A — listed in sub-genera and series groups.

Species	Common Name	Group, Pryor & Johnston	Major reduction in distribution	POTENTIAL CHANGE IN STATUS		
				Some site loss — less frequent	Gain or loss not clear	Major gain in colonisation
SUB-GENUS:						
MONOCALYPTUS						
Section: RENANTHERIA						
DIVERSIFOLIAE						
<i>Eucalyptus diversifolia</i>	Coastal white mallee	MABAC				
CAPITELLATAE						
<i>E. macrohyncha</i> , ssp. <i>macrohyncha</i>	Red stringybark	MAHACA				
OBLIQUAE						
<i>Eucalyptus pauciflora</i> , ssp. <i>pauciflora</i>	Snow gum	MAKHAA				
<i>Eucalyptus remota</i>	Mallee ash	MAKEB				
SUB-GENUS:						
SYMPHOMYRTUS						
Section: BISETARIA						
<i>Eucalyptus trivialis</i>	Victoria Spring mallee	SII:E				
<i>Eucalyptus cladocalyx</i>	Sugar gum	SIS:A				
<i>Eucalyptus oleosa</i>	Glossy red mallee	SIT:C				
<i>Eucalyptus socialis</i>	Red mallees	SIT:L				
<i>Eucalyptus yalensis</i>	Yalata mallee	SIT:M				
<i>Eucalyptus yumbarrana</i>	Yumbarr mallee	SIT:OA				
<i>Eucalyptus gracilis</i>	Yorrell	SIX:A				
<i>Eucalyptus calycogona</i>	Square-fruited mallee	SIX:D				
<i>Eucalyptus foecunda</i>	Slender-leaved mallee	SIZ:B				
DUMOSAE						
<i>Eucalyptus straticalyx</i>	Kopi mallee	SLE:F				
<i>Eucalyptus pileata</i>	Silver mallee	SLE:GB				
<i>Eucalyptus calcareana</i>	White mallee	SLE:GC				
<i>Eucalyptus cyanophylla</i>	Murraylands mallee	SLE:H				
<i>Eucalyptus concinna</i>	Victoria Desert mallee	SLE:I				
<i>Eucalyptus conglobata</i>	Cong mallee	SLE:IA				
<i>Eucalyptus anceps</i>	White mallee	SLE:IB				
TORQUATAE						
<i>Eucalyptus rugosa</i>	Kingscote mallee	SLI:A				
<i>Eucalyptus brachycalyx</i>	Gilja	SLI:B				
INCRASSATAE						
<i>Eucalyptus incrassata</i>	Ridge-fruited mallee	SLOAB				
<i>Eucalyptus angulosa</i>		SLOAC				
Section: EXSERTARIA						
TERETICORNES						
<i>Eucalyptus flindersii</i>	Grey mallee	SNEEK				

TABLE 3 Cont.

VIMINALE			
<i>Eucalyptus gonatocalyx</i>	Long-leaved box	SPIFB	
<i>Eucalyptus rubida</i>	Candlebark gum	SPIFI	
Section: ADNATARIA			
<i>Eucalyptus microcarpa</i>	Grey box	SUC:DB	
LARGILORENTES			
<i>E. largiflorens</i>	River box	SUDEC	✓
<i>Eucalyptus behriana</i>	Broad-leaved box	SUDGA	✓
INTERTEXTAE			
<i>Eucalyptus intertexta</i>	Gum-bark coolibah	SUH:A	
MOLUCCANAE			
<i>Eucalyptus albens</i>	White box	SUL:G	✓
ODORATAE			
<i>Eucalyptus porosa</i>	Mallee box	SUNCC	✓
<i>Eucalyptus lansdowneana</i> ssp.			
<i>lansdowneana</i>	Crimson mallee	SUNEA	
<i>E. lansdowneana</i> ssp. <i>albopurpurea</i>	Pt. Lincoln mallee	SUNEAB	✓
<i>Eucalyptus odorata</i> , var. <i>odorata</i>	Peppermint box	SUNEB	✓
<i>Eucalyptus odorata</i> , var. <i>angustifolia</i>	Peppermint box	SUNEBB	✓
<i>Eucalyptus viridis</i>	Green mallee	SUNEHA	
MELLODORAE			
<i>Eucalyptus leucosylon</i> , ssp. <i>primitiva</i>	Inland blue gum	SUN:CC	
<i>Eucalyptus petiolaris</i>	Eyre Pa. blue gum	SUN:CE	✓
<i>Eucalyptus leucosylon</i> , ssp. <i>leucosylon</i>	S.A. blue gum	SUN:CE	✓

The ecological significance of Goyder's Line

The practical limits to sustained primary production for land-use historically have been contentious and are likely to remain so. G. W. Goyder was put on his mettle to define such a boundary, which, all things considered, has been largely vindicated by time. He surveyed his line of demarcation for sustainable land use options in 1865 (McGowan 1990). He rode on horseback over 3000 miles (almost 5000 km) to define it. He associated the boundary with repeatedly observable facts related to the southernmost extension of drought as indicated by vegetation and soil features. These were the "chewed remains of saltbushes and other low shrubs" and "light soils which were susceptible to wind erosion" when dry, indicating silty-sandy textures and low contents of organic matter in the top soil. It has been alleged that he only surveyed the Upper- and Mid-north Regions but extrapolated his criteria to Eyre Peninsula and the Murray Mallee regions without specific attention being given to them. However, the boundary line in the central section, from near Moonta in the west to Eudunda in the east, is only 350 miles long. His extensive distance travelled for the survey demanded by the Government suggests he ventured much further afield to justify his boundary.

The Line, recognised as a broad limit, has come to be associated with three features, an average Winter rainfall of 220 mm, a rainfall/potential evaporation ratio of 0.26, (French 1989), and the southern extent of ecosystems dominated by saltbushes species; in particular *Maireana pyramidata* and *M. sedifolia*. None of these features alone is adequate to define the sustainable land-use criteria for the 20th century. Of particular concern here is whether its original joint-criteria will be assessable in time to serve in the latter half of the 21st century.

French (1989) showed that if the Winter (April-October) rainfall/evaporation ratio was to be maintained, the boundary associated with Goyder's Line would have to be located where the winter rainfall isohyet is currently 285 mm; i.e. shift some 70 km south of its present location on the plains of Eyre Peninsula and the Murray Mallee. Greenwood & Boardman (1989) assessed changes in growing season and net primary production in native ecosystems. The northern limit of low woodland, defined as ecosystems which increment new growth, under adequate conditions, of less than 2.2 dry t/ha/y would move south by about 100 km. These two independent estimates, considering the uncertainty, are in reasonable agreement. There is likely to be a drastic impact on vegetation. To the east of the Flinders Ranges the change indicates there would be a much more intense gradient of change from the hills to the plains than is presently the case.

Adaptations to greenhouse-induced climate change

One of the most difficult tasks for managers of land which grows long-lived plant species, trees and shrubs, especially where these species dominate ecosystems, is how to assess that change in environmental conditions is actually of significance to the present ecosystems, and what to do to ensure that the ecosystem, rather than the species themselves, can be maintained. Practical things to do which will make adaptation possible are limited by the indefinite nature of the time frames. It is difficult to make a positive contribution over such a protracted period without efforts being confounded by normal variation in weather and climate year by year. One positive suggestion being widely canvassed is mainly applicable to commercial tree species subject to improvement through breeding. This has been to progeny-test in areas which have a climate akin to the changes expected but currently outside the regions of economic viability.

The soil criteria adopted by Goyder can be ascertained on the basis of textural classification and degree of degradation associated with historic land-use and the rainfall quantity and evaporation trends should be discernible through use of running averages. Consequently, a future equivalent of Goyder's Line could be used to highlight the progress of climate change, should it eventuate.

Better definition of the boundary could be achieved with the selection of "indicator" plants, such as *Mairea pyramidifolia*, indicative of change in favourable or unfavourable environmental conditions, and good definition of the ecological factors which determine their limitations or provide for stability is needed. Ability of indicator species to colonise sites south and west of the current distribution should be priority subjects for ecology studies.

Another approach which has been adopted by Primary Industries SA-Forestry, that recognises forest and woodland have multiple-uses, has been installed (in 1992) near Gumeracha in a Demonstration Forest. This investigation has been designed to integrate both long-term and short-term benefits. Uses included are water supply catchment protection, agro-forestry and potential commercial forestry. Botanically closely-related land-races (provenances) and species, in five distinct groups of *Eucalyptus* similar in fashion to Table 3, have been matched to three climatic models. Trees

are being grown from seed collected (i) in good quality local populations in S.A., (ii) from central Victoria where the rainfall distribution pattern is like the postulated change, but the temperatures do not change, and (iii) and populations in the central part of eastern N.S.W. where rainfall distribution with a tendency to summer maxima and warmer temperatures occur. The flowering, seed set and natural regeneration phases of ecosystems, as mentioned above, are likely to be the most sensitive seral stages to significant climate change. The Gumeracha investigation aims to cover this eventually by providing genes in the dominant species which contain adaptation to climate in the directions in which it is very likely to change. The trial is providing a bank or nest-egg of genes to allow adaptation to occur whilst still likely to retain ecosystem structure associated with land-use.

A Forest Reserve at Whyte-Yarrowie, in the zone east of the southern Flinders ranges, which our studies indicate will suffer the most intense changes and increases in stress, has been reserved for scientific studies. One option we are considering is to plant a suite of 'indicator species', in range from those suited well at present to others growing in regions akin to the future climates of the scenario. Planting in a set design at ten-year interval for the next century would be immensely valuable in an ecological sense. Planting a bracket of three consecutive years at the decadal mark would help to reduce the effects of annual variation in weather. Such a programme calls for dedication, conscientious adherence to the plan and consistency to be adopted by managers, and lasting over several generations of ecologists. It may be too much to ask.

A second question concerns conservation of the current species composition of ecosystems which are valued and preserved in Conservation and National Parks. Greenwood & Boardman (1989) reviewed the impact of the median climate change scenario on the representativeness of Parks in S.A. There has been no significant addition to options suggested in 1988. Provision of gene banks and corridors of land able to permit species migration, mainly southwards is still seen to be the best option in the interim. In the absence of physical evidence to justify the need or conservation practices, sadly little has been added beyond revision of the Native Vegetation Clearance Act, to strengthen its preservation provisions, and to positively protect roadside native vegetation. There is still a need to include and emphasise whole-ecosystem conservation, and to modify current preference and emphasis on rare and endangered species.

APPENDIX I. Average annual temperature, annual rainfall and growing season estimates for recent times and the late 21st Century, adopting the IPCC 1991 median estimates of change in temperature and rainfall with latitude. Growing season length has been estimated with the De Marionne Drought Index from mean monthly rainfall and temperature data and estimates for recent times and the late 21st Century respectively (see Boardman, 1989).

Region	Weather Station	Mean Temperature		Average Rainfall		Growing Season months		Change in G.S. % of year
		Recent	Late 21C	Recent	Late 21C	Recent	Late 21C	
Eyre Pen.	Cleve	16.5	19.9	404	410	5.75	2.5	-28
	Ceduna	16.9	20.1	321	323	4.25	2.0	-19
	Polda	16.35	19.7	442	431	5.5	4.25	-11
	Kyancutta	17.0	20.3	330	330	4.25	2.0	-18
	Whyalla	18.0	21.35	273	293	1.25	0.5	-6
	Pt Lincoln	16.35	19.8	486	464	6.0	4.75	-10
	Kimba	16.55	19.85	346	352	4.75	1.5	-28
	Minnipa	17.2	20.45	325	323	4.0	1.0	-26
	Streaky Bay	17.45	20.75	378	360	4.5	3.25	-11
Yorke Pen.	Price	16.6	20.05	332	343	4.25	1.1	-26
	Warooka	16.05	19.55	450	433	6.0	4.5	-10
	Maitland	15.95	19.35	509	500	6.75	5.25	-12
	Kadina	16.65	20.05	396	395	5.25	2.75	-21
North:								
Upper	Hawker	17.65	20.85	301	311	3.5	<0.5	-27
Mid	Yongala	14.4	17.7	369	376	5.5	1.5	-34
	Bundaleer	14.8	17.1	554	544	7.0	7.0	±0
	Georgetown	16.05	19.35	468	466	6.5	5.0	-12
	Snowtown	16.4	19.7	407	405	6.0	3.0	-25
Lower	Kapunda	15.75	19.2	496	493	6.75	6.0	-6
	Roseworthy Coll.	16.35	19.8	439	443	6.5	4.5	-16
Murraylands	Milang	14.9	18.45	408	409	6.25	3.75	-21
	Nildottie	16.2	19.65	256	277	1.25	0	-10
	Wanbi	15.7	19.2	307	325	3.0	<0.5	-21
	Meningie	15.2	18.75	470	465	6.5	4.5	-16
	Wajkerné	16.7	20.1	311	342	1.75	0.75	-9
	Lameroo	15.55	19.05	393	400	5.5	3.0	-21
	Monarto	16.0	19.45	351	371	4.5	0.5	-33
	Mt Crawford	13.15	16.6	784	755	8.0	10.0	+16
	Myponga	13.6	17.05	763	734	7.5	10.0	+20
Upper SE	Bordertown	14.7	18.35	541	571	8.25	8.5	+2
	Keith	15.55	19.15	471	471	6.75	5.0	-14
Lower SE	Konetta	13.65	17.35	713	716	9.0	11.75	+23
	Naracoorte	14.35	18.05	586	580	8.0	9.0	+8
	Mt Burr	13.1	16.6	782	776	9.5	11.0	+13

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THE ECONOMIC IMPLICATIONS OF CLIMATE CHANGE

BY MICHAEL E. BURNS* & CLIFF WALSH†

Summary

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Feedback effects from the rest of the world on the economic structure and well being of South Australia are likely to be more significant than direct economic impacts of climate change in South Australia or even Australia as a whole. Economists can help to identify climate sensitive sectors of the economy and analyse how change in them will affect other sectors. Economists can also influence anthropogenic changes by prescribing appropriate incentive structure to redirect human actions in the common interest. Because of the nature of the data upon which economic models are built, their predictive capacity is restricted to short periods of 1-5 years. It is postulated that areas such as agriculture, forestry, fishing and hunting would be highly sensitive to climate change whilst electricity, gas and water, construction, recreational and other personal services together with ownership of dwellings would be only moderately sensitive. Mining, manufacturing, wholesale and retail trade, transport, storage and communications, public administration and community services, finance, property and business services would be negligibly sensitive to predicted climate change. The problems associated with control of greenhouse gas emissions in an economic framework are controversial and difficult to resolve in a global context and the significance of collaborative approaches to these and other problems cannot be overemphasised.

Key Words: Climate change, economics, greenhouse gas emissions, anthropogenic influence, economic models.

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KEY WORDS climate change, economics, greenhouse gas emissions, anthropogenic influence, economic models

Introduction

An important feature of the symposium for which this paper initially was prepared was the bringing together of at least a little more information about the likely regional and local effects of climate change (beyond very tentative material available from the Greenhouse '88 Adelaide workshop and elsewhere). The contribution economists can make doesn't depend totally on this information, however. Like other sciences (social as well as physical), economics can contribute to discussion and debate through increasing understanding and application of its way of thinking about issues and problems. We are not here referring to the common view that economists insist on reducing everything to dollars and cents. Rather, we mean the more general contribution that economics can make through its development of frameworks for evaluating public policy options which:

- emphasise costs as well as benefits of policy action;
- pay particular attention to incentive structures in policy design;
- recognise how the actions of one individual, enterprise, region or nation impact on others; and
- notwithstanding the usual presumption that economists think that markets work perfectly, acknowledge cases where "the invisible hand" of the market is either arthritic or non-existent, such as when there are spillover effects, poorly defined property rights, high transactions costs, or the need

to impute "existence values" (eg. of life on earth) exists, and design policies to moderate their consequences.

Moreover, like those physical scientists who are deeply engaged in attempting to understand climate change and the role of greenhouse gases in it, the economists' framework is general equilibrium in nature and, to the greatest extent possible and necessary for the problem at hand, it is **global** in its recognition of impacts. To be more specific, the economists' modelling includes feedback effects between markets, including from world markets.

This observation leads to our first, simple, and yet profoundly significant point about the economic implications of climate change. That is, for a small region like S.A., with a not highly unusual economic and physical structure, feedback effects on our economic structure and well being from the rest of the world are likely to be more significant than direct economic impacts of climate change within South Australia, or even Australia as a whole.

On the basis of modelling of various scenarios produced in late 1980's, estimates of the loss of World output and income (often extrapolations from specific country studies, especially the USA) ranged from 1%-6% of GDP for temperature increases in the range 2-10 degrees Celsius. These are very large output and income changes in absolute terms, and their effects on growth of demand for South Australian products would be very substantial and likely to outweigh any direct adverse effects of climate change in South Australia on South Australian production and incomes.

The estimates of climate change, however, remain highly uncertain and have tended to be progressively

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reduced in more recent years. The uncertainties about whether, when and how climate change will occur, moreover, are compounded by the fact that they are based on a presumption that policies will not change soon enough, or sufficiently, to alter outcomes. Predicting policy responses is as important, in the end, as predicting climate change itself.

Uncertainties in climate prediction: the policy feedback issue

Others are better qualified than us to explain the nature of the models being used to generate climate predictions based on observed trends in greenhouse gas emissions, and the uncertainties that surround them. What we might usefully focus some attention on, however, is the inter-related issue of policy feedbacks.

The economic projections of the consequence of climate change that currently exist are based on a "worst case" policy scenario of no significant change in policy in response to emerging, or anticipated, climate changes. This degree of pessimism may be unwarranted, but climate change certainly involves some characteristics which give pessimistic outcomes a higher (than usual) weight in probability distributions defined over likely responses.

Policy responses to climate change have characteristics similar to what economists, in other contexts, call public goods. For example, in the familiar case of a system of national defence, once a unit of "protection" is provided for one person it is simultaneously provided for all others, and those unwilling to contribute to the costs cannot be excluded from benefits. In large numbers context, individuals see themselves as having negligible impact on quantities produced whether they offer to contribute to costs or not, and therefore the rational response is to attempt to free ride. Even though all others may do likewise, and nothing is produced as a result, it still will not pay to offer to contribute because whether you do or not generally will not affect decisions of others. This is a classic case of market failure, and a case where government provision, funded through compulsory taxes, is inevitable and desirable.

It should be noted, nonetheless, that even in the relatively simple case of defence, giving governments "the power to coerce" does not ensure that an optimal quantity of defence will be produced. Voting, lobbying and other means by which people signal their preferences in the political market have peculiar characteristics, and the incentive structures facing political and bureaucratic decision-makers have a tendency to encourage oversupply of public sector goods and services.

Clearly, policies to control climate change have the same characteristics as defence: effective action will benefit all nations, whether or not they contribute to the cost (financially and/or their own policy actions). They also face the added complexity, of course, that a government does not exist that can coerce nation states to pursue policy changes. We have to rely on international cooperation, a notoriously rare phenomenon, pursued through complex procedures, which is likely to see countries and groups holding out (free riding) at others' expense — even when perceptions of the likely costs of failure to obtain agreement are broadly agreed to be high. The deferred nature of the likely costs of global warming, even if agreed to be inevitable, add further difficulties of getting cooperation.

This is not intended to be totally pessimistic — just to reinforce what common experience (if not common sense) predicts about global policy change. Given scientific uncertainties, watchful caution about global action is desirable anyway. The classic example of Thomas Malthus' 18th Century prediction that global population would grow exponentially but food production only arithmetically, and the failed Club of Rome predictions in the 1960s, serve as eloquent warnings against precipitate policy responses. On a more optimistic note, there is some evidence that free-rider behaviour gives way to greater cooperation when the stakes are agreed to be very high, if only for fear that failure to participate or contribute will result in retaliatory action.

In all likelihood, the less developed world (LDC's) will be less willing to bear the cost of policy change, and more likely to stay outside any agreements, even though they also are more likely to use technologies which are inefficient from the viewpoint of greenhouse gas (GG) emissions. One consequence of this is that the "price" the developed world, South Australia and Australia included, has to pay might be not just the cost of reducing emissions in their own areas, but also substantial resource transfers to LDC's to buy their participation. Those costs are likely to be high even without transfers to LDC's: it has been suggested, for example, that reducing greenhouse gas emissions by the order proposed under the Commonwealth's 1990 interim planning target would be cost 1-3% of Australia's GDP (IC 1991).

Despite the lack of accurate and detailed predictions about climate change, about which elements are due to human actions, and in what ways policy-makers world-wide are likely to respond, there are still a number of ways in which economists can usefully contribute to the debate. For one thing, they can help to identify climate sensitive sectors of the economy and analyse how changes in them will affect other sectors.

TABLE 1 *Breakdown of South Australian gross state product and employment by sensitivity to climate change, 1990-91*

Sector	GSP		Employment	
	Value \$m	% of total	No. ('000s)	%
State Total	25,214		636	
High Sensitivity		3		7
Agriculture, forestry, fishing and hunting	834	3	43	7
Moderate sensitivity		24		11
Electricity, gas and water	688	3	8.9	1
Construction	2,003	8	37.1	6
Recreation, personal and other services	1,005	4	22.8	
Ownership of dwellings	2,346	9	n.a	
Negligible sensitivity		73		83
Mining	755	3	3.6	1
Manufacturing	4,746	19	105.6	17
Wholesale and retail trade	3,571	14	135.8	21
Transport, storage and communication	1,975	8	35.8	6
Public Administration and Community Services	5,258	21	181.2	28
Finance, property and business services	1,972	8	62.1	10

Identifying sensitive areas and relevant flow-on effects

Economists have their own range of "global models" aimed at capturing the interactions between markets within and across countries. As in other areas of modelling, there are well-understood limitations associated with the use of models. For one thing, for operational reasons (tractability of solutions, etc.), there are trade-offs between the level of disaggregation and detail, the richness of the dynamic specification and feedback mechanisms, and the complexity of the functional forms used to describe decision-making behaviour. For another, not only are data limited, but laboratory experimentation and replication of experiments are not generally possible. Moreover, because of technological, climatic, political and population changes and so on, many of the parameters of an economic model also will change over time: depending on the variables in question, useful predictions may only be made for the very short-run (1-5 years ahead).

Subject to the above reservations, however, it is possible both to identify qualitatively those parts of the economy (and of other countries' economies) which are most sensitive to climatic change and to discuss generally how changes in the affected sectors might flow-on through the economy as a whole. A simple approach, illustrated in Table 1 is to consider a breakdown of the economic activity of a region such as South Australia into the output and employment contribution of different industry sectors, noting the sensitivity of each sector to climatic change. (We follow the classification of sectors adopted by IC 1991).

With more detailed climate scenarios for South Australia, beyond those yet able to be provided, we can further refine this classification as well as get into more specifics. For example, we could track the impact on other sectors which supply inputs to agriculture of a climate-induced change in agricultural output through the use of input-output (or, preferably, computable general equilibrium) models. It is important to note that the relevant analysis must take into account the global economy. To illustrate this, while agriculture may be hurt (it may also become more productive) in Australia, because it is hurt elsewhere such as China, India or the USA, Australian exports may become more valuable and Australians become better off, even though total Australian production is reduced. By the same token, however, if other countries become poorer, the value of our exports could diminish. Sorting out these issues clearly is vital to understanding the consequences of climate change for us, and globally (since we assume South Australians have the well-being of others as part of their concerns).

The need to take into account the global international trade interactions has already been the subject of analysis and research by economists in North America and Europe. At the most recent meetings of the prestigious American Economic Association, an entire session was given over to Greenhouse Warming considerations. At this session, Reilly & Hohmann (1993), explored the agricultural effect of climatic change and the worldwide trade implications of a range of scenarios. Despite the global nature of the approach adopted, the authors' work contributes significantly to the identifying of key impacts and flow-on effects for South Australia.

The analysis by Reilly & Hohmann, through its analysis of the interactions of global regions (North

América, European Community, former Soviet Union, northern Europe, China, Japan, Australia, Argentina, Brazil and "Rest of World"), gives powerful illustration of the complexity of climatic change effects upon an individual region. Thus, Argentina was predicted to benefit overall, even though no increase in agricultural production was expected in that country and their domestic agricultural prices were expected to increase (in line with international prices).

Evaluate particular scenarios

As was done by CSIRO (1988 and revised 1992) specific (and moderately plausible) climate change scenarios can be considered. The major characteristics of these scenarios for the Australian region are set out in Table 2.

Using the most recent of these, a group of economics graduates (Hutchins *et al.* 1993) in a project for South Australian Department of Environment and Land Management, estimated a loss of 20% in volume and value of South Australia's wheat production. The conclusion regarding value, must be treated with a great deal of caution, however, bearing in mind our earlier discussion of the importance of taking into account global trade interactions.

The results of such exercises have led to two further tentative explorations. First, there has been use of general equilibrium economic models, such as ORANI, to examine the consequences of reduced wheat yields, increased forestry and fishery productivity and so on. Second, there have been evaluations of some of the more extreme sources of costs due to flooding, droughts and cyclones (an evaluation of costs, of course, opens upon considerations of costs of "abatement").

The first of these approaches, embedding the predicted effects of climatic change into supply shocks in the agricultural sector of (national and global) economic models, has been widely used. Comparison of the results of such different research programs is difficult, however, not least because the continuing uncertainty about the direction and magnitude of climatic change has resulted in quite different scenarios being considered from one study to another.

As an example, the previously cited work of Reilly & Hohmann draws on the climate change forecasts summarised in Houghton *et al.* 1990. The general scenario, which involves temperature increases of 2°C in the tropics and in the range 4°C to 12°C for the polar regions, has agricultural productivity increasing in the North of the (former) Soviet Union, Canada and Europe, but reducing in the United States and most of the rest of Europe due to drought (see Tobey *et al.* 1992).

In addition to incorporating economic feedback mechanisms and international trade linkages, some attempt has also been made to extend the interface between the economy and the environment by embodying possible agricultural sector responses. Questions of "adaptation potential" and "adaptation capability" are considered to bear, respectively, upon crop substitutions that are potentially available and desirable due to climatic change, and upon the constraints to these substitutions due to poorly developed markets for crop inputs and a range of infrastructure considerations, including the skill level of the agricultural labour force.

TABLE 2. CSIRO climate change scenarios 1987 and 1992. Scenarios for year 2030. Sources: Pearman (1988) and Climate Change Group (1992).

	1987	1992
TEMPERATURE	-2 to 4°C	+0.5 to 2.5°C
RAINFALL	-50% in north -20% in south	Summer 0 to +20% Winter SA 0 to -10% SE Aust -10 to -10%
RAINFALL INTENSITY	20-30% increase	General increase
SEA LEVEL	+20 to 140 cm	-5 to 35 cm
TROPICAL CYCLONES	Extend 200-400 km further south Frequency increase 30-60%	Uncertain
SNOW LINE	Rise 100 m per 1°C warming	Rise 100 m per 1°C warming
WIND SPEEDS	Decrease 20% North of 36°S Increase south of 36°S	Strengthening of monsoon westerlies in north Aust. & the SE trade winds in summer.

Insights into the occurrence of anthropogenic changes

None of the analyses considered so far distinguishes between changes due to human actions and changes which have other causes. It appears to be true that, by accident or otherwise, human impacts on climate, so far (and for some time ahead), may have made things better for humans than would otherwise have been the case. There is also the fact that, to some extent, the living world adapts to new conditions.

These possibilities apart, it is well understood by economists that individuals will sometimes impact on their environment in a way that reduces the common good, through, for example:

- externalities (spillover effects);
- inadequately defined property rights
- transaction costs
- failure to recognise "existence values" (e.g. of life on earth).

For such cases, economists also are able to prescribe the appropriate incentive structure to redirect human actions in the common interest.

Externalities occur where the actions of one decision-maker impose costs (or bestow benefits) upon other individuals. Problems occur when the relevant decision-maker is not required to take into account these external costs (or benefits), so that an inappropriate level of an activity is undertaken. As an example, a manufacturer, in the course of generating income, may use a process that involves significant GG emissions. Suppose that these emissions lead (over time) to a climatic change which reduces global agricultural productivity and results in a range of price increases of basic commodities. Because the manufacturer's decision whether to produce or not does not have to take into account the (external) costs imposed upon others, a situation can arise where the value of a manufacturer's output, over and above the (internal) costs of production, is less than the costs imposed upon the rest of the community through the impacts upon agriculture. A tax on emissions would encourage the manufacturer to behave in a socially preferred way.

Whether the presence of externalities is a major problem in practice frequently depends upon how well defined are the property rights of a particular resource. Ownership of resources such as air, water and other facets of the natural environment, for a variety of reasons, often is poorly defined. If it is not defined in law who owns a particular resource, then consumers of the resource are without legal recourse when the quality and quantity of the resource is reduced due to the actions of others. With regard to the earlier example, agricultural producers are not in position to sue the manufacturer(s) for a loss in productivity brought about by increased GG emissions.

It might seem that externality problems can be handled by the simple act of ensuring that the ownership of resources (such as air and water, etc.) is fully defined under the law. Leaving aside for the moment obvious legal complexities, if, for example, the agricultural sector was given property rights over the atmosphere, that sector could (in theory) sue the manufacturer for the costs due to GG emissions. Even if the manufacturer was granted property rights over the atmosphere, then (in theory) a better outcome could be obtained as the agricultural producers could decide to pay the manufacturer to decrease production or to invest in a cleaner process. (This may seem "unfair", but it would result in more socially efficient outcomes).

It is, perhaps, useful to remember here that economists do not prescribe zero emission of GG's or, in general, zero levels of any other form of "pollution". Most anthropogenic activities are "polluting" or have externalities to some degree and economists see the problem as balancing (on the margin) the full costs (including externalities) of an activity with the benefits of that activity. The assignment of property rights can go some way to seeing that decisions about activity levels take some account of externalities.

This question of identifying and taking appropriate account all relevant costs is central to the economist's trade. It also leads directly to a further complication in the treatment of externality-producing activities. Even if property rights could be clearly defined, there may be substantial transactions costs involved in obtaining the desired outcome. With regard to the emissions of GG's, which manufacturers are responsible for which proportions of the emissions, and how much are individual agricultural producers affected (and by whom)? At the very least, there could be very substantial monitoring costs involved, and these would be "compounded" by further legal and administrative costs. As a result, the costs of identifying and achieving appropriate levels of GG emissions may be greater than any benefits obtained. Economists must design policies that take into account the costs of administering the policy. It is for this reason that a range of other policy-measures are often considered, such as "pollution" taxes or deterrent fines. The proposed hydro-carbon tax, considered in more detail below, is one such example.

Consideration of factors such as these give insight as to why ordinary decent citizens of planet Earth may make decisions that are rational for their individual selves, but contrary to the global good. Understanding these factors also is necessary for policy design, but unfortunately may not be sufficient. Policy parameters can only be set on the basis of agreed valuations of current and future states of the world. Such estimates must include valuations of quite complex items, such as environmental resources or even "life on earth". The difficulties here include the absence of, or irrelevance

of a simple market value and the question of how the future should be valued relative to the present time (the choice of a discount rate).

The difficulties in evaluating assets such as the Great Barrier Reef or Antarctica are well understood. The private auction of a communal good will always ignore the values held by individuals who will be excluded from use of the asset: the imputation of value on the basis of current use of a resource ignores both the "option values" of those who would value the opportunity to possibly use a resource in future and the "existence values" held by those, for example, who will never use a resource in any way but who simply value its presence and preservation.

Analysis of alternative policy measures

Insights into the reasons why human actions are likely to lead to undesirable levels of greenhouse gas emission and associated climate change, such as those discussed above, enable economists to prescribe incentive structures which will redirect human actions toward the common interest. There are obvious informational obstacles to the determination of such incentive structures, as can be illustrated by brief consideration of an "ideal" data situation.

Clearly, it would be useful if it was known exactly: how the emissions associated with different production processes and consumption activities impacted upon future production and consumption; the "taste" parameters of the population that describe the relationships between consumer choice and prices; and, other factors, such as the structures of the different markets in the economy and the policy objectives of domestic and foreign governments. If all of this was known, then, as in any other closed equilibrium system whose descriptive parameters are known, an optimal intervention strategy could be conceptualised and derived.

In practice, the framework within which we have to work has at best only some stable parameters and a range of stochastic elements. Furthermore, whatever stable parameters may exist are not known with certainty but must be estimated, and the precision of such estimates is itself dependent upon our understanding of the nature of the framework itself. Of course, no less is true regarding the estimation of the parameters of systems in the physical sciences.

The impact of all of this uncertainty is that economic policy prescription often best can be thought of as being a two stage process. First, largely on the basis of theoretical considerations, it is possible to make qualitative prescriptions that will be robust with respect to a number of alternative models and parameters describing real world behaviour. The general suggestion, referred to above, that a hydro-carbon tax

would reduce the incentive for participation in activities which contribute significantly to GHG emissions and climatic change, is an example of a reasonably robust qualitative policy prescription.

The second stage is the more difficult. It is one thing to be aware that a hydro-carbon tax can impact upon behaviour in a desirable manner, but it is quite another to know what size tax should be used and on what particular commodities. It is to obtain insights into this latter question that much current economic policy research is directed. At the recent American Economics Association meeting mentioned earlier, two examples were provided of this kind of research activity. Not surprisingly, both papers use models embodying gross simplification of the global economic and climatic interface.

In Nordhaus (1993), dynamic integrated climate-economy (DICE) models are extended "... by integrating the economic costs and benefits of GHG reductions with a simple dynamic representation of the scientific links of emissions, concentrations and climate change" (Nordhaus, 1993 pp. 313). Conditional upon an estimated loss in overall National Product of 1% for every 3°C warming, Nordhaus' study suggests that the optimal carbon-tax policy would involve an initial tax of just over \$5 per ton, rising steadily over time to reach about \$20 per ton (based on current prices) by the end of the next century. It is estimated that the net benefits, globally, of such a policy compared to doing nothing would be of the order of \$16 billion annually. More significant is the conclusion that the popularly recommended immediate cut of GHG emissions (relative to 1990) would require an initial tax of \$56 per ton and overall, compared to a no-control situation, would actually involve a global cost of over \$750 billion annually.

Economic policy, whether to do with GHG emissions or otherwise, is in itself a complicated and controversial issue. There has been much argument that public bodies are inefficient in their own activities and that tax revenues are badly used. It is also widely accepted that most taxes, including many existing ones, cause inefficiencies in the economy as a whole by preventing the price system from signalling the "true" values of commodities and resources. With respect to issues such as these, Nordhaus makes two interesting observations with respect to the imposition of even the "optimal" rate of tax on appropriate commodities. First, if the tax revenues are used with a plausible level of inefficiency in the public sector, all benefits due to GHG emission reduction may be totally outweighed. Second, however, if these tax revenues could be used to eliminate existing taxes which were distorting the price mechanism in a costly manner, the annualised global benefits might increase from \$16 billion to over \$250 billion.

The above is useful in that it gives a flavour of how economists approach the integrated analysis of climate and the economy over time. It also indicates that no single economic policy can be considered in isolation from other government interventions in the economy. What the discussion fails to convey, however, is the scale of the uncertainties which economists admit to in this area of investigation.

Gaskins & Weyant (1993) offer a vivid, if perhaps extreme, illustration of this uncertainty. In their comparison of 14 "DICE-type" models and 13 climatic scenarios, estimates of the average carbon tax required over the period 2000-2020 to achieve, for example, a 20% reduction in carbon emissions (compared to 1990) vary from \$50 per ton to \$330 per ton. In fairness, extreme estimates tend to flow from extreme assumption underlying alternative models and a fundamental aspect of model development is to identify the potentially sensitive areas and to refine the accuracy and level of agreement regarding these areas.

Other policy evaluation exercises, in many ways simpler, are undertaken by economists, including the previously cited approaches using the ORANI model. This model is a highly disaggregated general equilibrium model of output, employment and consumption in the many different sectors and regions of the Australian economy. It would not be operationally feasible to construct a DICE model at this level of detail, but what ORANI can do is predict, for a given well-defined policy initiative, the likely micro-effects across the regions of the economy. To know in advance, for example, that a particular section of the Adelaide metropolitan region is likely to experience significant unemployment because of GG policy measures, can be of significant use to social planners.

Conclusion

The capacity of economists to provide clear predictions of the costs and benefits of climate change, or of policies to modify likely future climate changes is limited by a number of factors, not least the uncertainties surrounding predictions of climate change. The work done so far is slight and highly speculative, but it has grown — and in collaboration with our colleagues in the physical and health sciences, for example, it could further expand in extent and value to the policy process — especially as the world works its way out of the problems of recession that have thoroughly captured the attention of policy-makers in recent years.

The significance of collaborative approaches cannot be over-emphasised. Especially in areas where extant knowledge is very limited, and subject to a very high degree of uncertainty, it can ensure that research and modelling investments by different disciplines are mutually supportive. Because of the nature of their "business", economists bring not only analytical and modelling skills to the consideration of issues such as climate change, but also a sharp focus on what is "policy-relevant" information and analysis.

Contrary to the belief of many, if not most, non-economists, economists do not believe that private sector markets always work well and provide the right signals and incentives. But their scepticism about private markets applies equally to political markets where lobbying has a powerful role, and where regulations can become captured by those they are supposed to regulate. An early keen eye to these issues can result in policy debate and design being focussed on achieving better ultimate policy outcomes at lower cost.

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CLIMATE CHANGE AND HUMAN POPULATION HEALTH: GLOBAL AND SOUTH AUSTRALIAN PERSPECTIVES

By A. J. McMichael† & M. Y. Beers*‡*

Summary

McMichael, A. J. & Beers, M. Y. (1994) Climate change and human population health: global and South Australian perspectives. *Trans. R. Soc. S. Aust.* 118(1), 91-98, 31 May, 1994.

Public health scientists now need to think within an ecological framework because of planetary overload by the human species. Climate change must impact on human health. Predicted health hazards include increases in thermal extremes which impact particularly on the very old and the very young. Natural disasters such as cyclones, floods and ocean storm surges will increase rates of injury and death. Insect and other vectors for infectious diseases will change geographic distribution resulting in changes in the demography of diseases such as malaria, yellow fever, dengue, encephalitis and cholera. Changes to agricultural productivity will alter food availability in many regions. Rising seas would, amongst problems, disrupt sewage disposal causing diarrhoeal diseases. Climate-induced environmental disruptions would create "ecological refugees" leading to spread of infectious diseases and social disorganisation. Ozone depletion with increased exposure to ultraviolet radiation will lead to an increase in skin cancers, eye disorders and immune suppression. The significant environmental degradation in South Australia, together with climate change could lead to significant increases in water pollution, outbreaks of Ross River virus, Murray Valley encephalitis, dengue fever, tick-borne diseases and possibly Hanta viruses together with gastrointestinal diseases.

Key Words: global environmental change, human ecology, human population health.

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Introduction

During its quarter-million years of existence, *Homo sapiens* has adjusted to several shifts in the prevailing profile of environmental health hazards. Each shift has coincided with culturally-driven changes in the social organisation and ecological relationships of the human species: the advent of agriculture, urban settlement, industrialisation, and the spread of "affluent" living. Today, another category of environmental health hazard is emerging that is qualitatively distinct from earlier hazards and may well have wider-ranging health consequences. This hazard arises from the planetary overload resulting from the cumulative impact of the human species, via population growth, land pressures, energy-intensive technology and a high output of waste gases – including changing the gaseous composition of the lower atmosphere and, hence, its heat-trapping properties (McMichael 1993).

Appraisal of the health hazards of these incipient global environmental changes requires us to think within an ecological framework. Public health scientists have not heeded this framework previously because, until recently, humans were (apparently)

living within the biosphere's carrying capacity. Now, however, there are signs that our aggregate impact is reducing the stability and productivity of various of Earth's natural life-supporting systems. Each of these individual problem areas is already a familiar subject of environmental research and debate: greenhouse gas accumulation, stratospheric ozone loss, land degradation, aquifer drawdown, depletion of ocean fisheries, loss of biodiversity, and the ecological and social consequences of rapid urbanisation. But their wider, collective, *ecological* significance for human population health has been rarely considered.

There is much that is uncertain – and controversial – about the causation, course and consequences of global environmental changes. This has been well demonstrated by the divergent views of scientists about the net impact of greenhouse gas accumulation upon the world's climate. The consequent difficulty for health researchers is knowing whether and how to reap further uncertainties about health outcomes upon the underlying uncertainties about global-change processes. Nevertheless, since sustained overload of the biosphere must, logically and eventually, entail a reduction of its life-supporting ability, it is a reasonable, and prudent, inference that this poses a fundamental hazard to human health. Estimations of health impact must therefore be attempted.

The best-documented and most discussed aspects of global environmental change are those pertaining to climate change. "Climate change" has been widely taken to include both greenhouse enhancement and ozone depletion. Purists may argue that "climate" is a tropospheric phenomenon, and has to do with

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temperature, precipitation, humidity and winds; since ozone depletion is occurring in the stratosphere, and its main anticipated consequence is an increase in surface-level ultraviolet irradiation, it is not part of the climate change. However, the demarcation is not clearcut — there are various interactive and other relations between these two processes. For example, chlorofluorocarbons (CFCs) contribute to both processes; tropospheric warming may enhance stratospheric cooling; and ozone depletion may affect the radiative forcing properties of the atmosphere overall. In this paper we use the inclusive approach.

Two other qualifying comments are needed here. First, specifying the adverse health effects of climate change rests largely on extrapolation and, in some cases, reasonable conjecture (McMichael 1993; Maskell 1993). Unlike the directly toxicological hazards posed by localised environmental pollutants, this category of health hazard does not readily permit the empirical observation of health impact in one population as a basis for estimating the risk in other populations. As more information about these complex systems accrues, the modelling of population health impacts will improve.

Second, it is generally difficult to make predictions of localised effects of climate change upon the health of South Australians. For certain, simpler, processes — such as skin cancer risks due to increased ultraviolet irradiation (UVR) and the change in mortality due to increased frequency of heatwaves — local estimates can be made, but for many other processes (e.g. effects upon regional and global food production) the health of South Australians will reflect their sharing of the experiences of wider populations. Therefore, this paper concentrates initially upon the general possibilities of population health impact, after which some more specific comments are made about the South Australian context.

Greenhouse gases and climate change

Various natural "greenhouse" gases in the lower atmosphere absorb much of the heat that is re-radiated from the Earth's surface. Fossil fuel combustion and accelerated forest clearance since 1800 has increased the concentration of carbon dioxide from 275 ppm to 360 ppm. Concentrations of other anthropogenic greenhouse gases, especially methane and the chlorofluorocarbons (CFCs), are also increasing (IPCC 1992; Epstein 1992).

The United Nations Intergovernmental Panel on Climate Change (IPCC) estimates that, in consequence of the increase in radiative forcing, the average global temperature will rise by around 2–3°C by the year 2100 (IPCC 1992). While this estimate is acknowledged to be uncertain, the evidence is firming that human activity is now warming the Earth's surface (Lacis &

Carlson 1992). A rapid global temperature increase of several degrees would be without precedent in all of human history, and would pose a range of risks to human health, both by direct and (probably more important) indirect mechanisms (Last 1991). The 4–5°C increase in temperature after the more recent ice age which (several smaller fluctuations aside) occurred over several thousand years, caused major ecological changes — including the spread of forests and, together with intensified human predation, the extinction of many large mammals; it also presumably contributed to the onset of agriculture.

The most likely impacts of greenhouse-induced climate change are summarised in Table 1.

TABLE 1. Main potential effects of global climate change on population health.

Direct	Increased frequency of heatwaves → deaths, illness, injury. Respiratory effects of moisture, dusts, pollens. Climate instability → disasters (cyclones, floods, fires).
Indirect	Altered habitat and transmission of vector borne infectious diseases (other contagious diseases also). Impaired crop production (soil, temperature, water, pests). Sea-level rise — inundation; sanitation, salinity, etc. Demographic disruption, environmental refugees.

The main direct hazard to health from a temperature increase comes from thermal extremes. It is predicted that the frequency of heatwaves in temperate and sub-tropical climates will increase (Brasseur 1991) — for example, a doubling in the annual number of days over 38°C in Washington, DC, is predicted over the next half-century (Leef 1989). It is not unusual in temperate zones, such as South Australia, for three to four days each summer to record temperatures greater than 38°C. However, with an average annual temperature increase of 2–3°C, the number of days in excess of 38°C is predicted to rise (Ewan *et al.* 1991).

In response, death rates among the most susceptible, particularly the very old and very young, will rise (McFarlane 1978; Kilbourne 1992). Causes of death to rise would include heat-stroke, exhaustion, cerebrovascular stroke and, probably, accidents and acts of violence. On the other hand, winter deaths from influenza and from hypothermia — particularly among the homeless poor from Delhi to London to New York — could be expected to decrease.

Weather patterns are likely to be destabilised, with more frequent cyclones, floods and ocean storm surges. These "natural" disasters would increase rates of injury and death. They would also disrupt agriculture, local transport and sanitary engineering. Fringe dwellers in

flimsy housing or exposed to rivers and oceans, as in coastal Bangladesh, will be the most vulnerable (Houghton *et al.* 1990). In Australia, it is predicted that cyclonic activity would extend down the eastern coast from a latitude band of 27°S to 31°S (Australian Bureau of Statistics 1992). However, there are unlikely to be consequences for Australia's southern coastline.

Various insects, vertebrates and other vectors for infectious disease will change their geographic distribution (Cook 1992; Shope 1992). As higher-latitude locations become warmer and wetter, mosquitoes will tend to spread there. As well as extending their spread and seasonality in tropical countries, mosquito-borne infections (malaria, yellow fever, dengue, and various forms of encephalitis) may return to currently unaffected temperate areas. (Ancient Rome and early Europe were malarious; so, earlier this century, were parts of the United States, England, Italy and northern Australia.) Vector-borne diseases spread by flies, water-snails and vertebrate animals are also likely to change their distributions. Recent evidence that cholera is "vector-borne", by taking refuge under the mucinous outer coat of aquatic algae (including species found in both fresh and coastal waters), suggests that its spread may also be assisted by warmer oceans (Epstein 1992).

Long-term increases in background temperature may reduce the yield of some of the world's most productive grain-growing temperate regions – the American prairies, western Europe, the Ukraine and coastal Australia – while increasing the agricultural productivity of other regions (northern Europe and Canada) (IPCC 1990). Crops that have been selectively bred for specific environments, may fail to germinate. Climate change may also alter habitats for those insects, fungi and micro-organisms that cause "diseases" of grains, fruits and vegetables. While increased levels of carbon dioxide in the atmosphere may enhance plant growth (especially the evolutionary older "C3" plants), most current evidence indicates that, on balance, this would not be a significant effect. Further, while the overall net effect of climate change upon world agriculture is uncertain (Parry 1990; Crosson 1989) at a regional level food security may be seriously threatened – especially in poorer countries in the semi-arid and humid tropics. Climatic change would also perturb the growth and productivity of livestock and fish, local fuelwood supplies and the availability of freshwater – all important determinants of health.

A rise in sea levels is predicted from thermal expansion of the ocean. The IPCC estimates a rise of approximately 0.65 metres by the year 2100, with serious effects upon low-lying coastal communities. The most vulnerable settlements are those in coastal lowlands such as in Bangladesh, China and Egypt, and in small island nations. Inundation and storm surges

could lead to significant displacement of people (Maskell *et al.* 1993; Worrest & Grant 1989). Rising seas would also disrupt sewage disposal (thus causing diarrhoeal diseases), cause increased salinity of coastal freshwater estuaries and farmlands, and harm wetlands and the breeding grounds of many ocean fish (Haines & Fuchs 1991).

Many of these climate-based environmental disruptions would create "ecological refugees" (Jacobson 1989). Dispossessed people from areas damaged by floods, cyclones, rising seas or droughts would migrate to the relative safety of cities. Shanty towns would proliferate – and so would infectious diseases and social disorganisation. It is conceivable if climatic and agricultural and demographic circumstances deteriorate significantly in the coming century, that Australia will have an influx – voluntarily or even uncontrollably – of refugees from Southeast Asia.

Ozone layer depletion

Stratospheric ozone, which resides at 10–20 km altitude, accumulated over several billion years principally as a result of the evolution of oxygen-releasing photosynthesis. This ozone "layer" provides life on Earth with substantial protection from biologically-damaging UVR (particularly the higher-energy UV-C which is entirely absorbed and the medium-energy UV-B which is largely absorbed). Today, the stratospheric ozone is being damaged by human-made chlorofluorocarbons (CFCs) and other industrial gaseous emissions.

At mid-northern latitudes (30–50°N) the ozone layer thinned progressively by around 0.5% per year during the 1980s and early 1990s (Stolarski *et al.* 1991; Brasseur 1991; UNEP 1991). Overall, during that period there was an accumulated 8% loss in winter and a 2% loss in summer. Meanwhile, in the southern hemisphere, significant cumulative ozone loss occurred during the 1980s from the pole "down" to latitude 30°S, which includes the lower parts of Australia and of South America. There now appear to be well-established, strengthening trends in ozone depletion in both hemispheres. The anticipated increases in UV irradiance at ground-level would be greatest in the southern parts of Africa, Australia and South America and in the mid-latitudes (30–60°N) in Europe, Asia and North America (Madronich 1992).

The predicted direct effects of increased human exposure to UVR include increases in skin cancers, eye disorders, and suppressive effects upon the immune system. The UN Environment Programme estimates that for every 1% decrease in ozone, there is an approximately 1.5% increase in exposure to ultraviolet-B (UV-B) radiation at the Earth's surface; in turn, each sustained 1% increase in UV-B would cause an

estimated 2-3% increase in the incidence of skin cancers, predominantly non-melanoma cancers. Increased UV-B exposure is also predicted to increase the occurrence of cataracts and of pterygia (tissue overgrowths on the cornea) (Taylor 1989). Less certainly, it may depress the body's immune system, thus reducing protection against infectious and fungal diseases (Morison 1989). Although there has been frequent reference to these various predicted health outcomes, the estimated increases in incidence are based on rather sparse data (Armstrong *in press*).

During 1993, an attempt was made in Australia to predict the number of extra UVR-induced cases of skin cancer — basal and squamous cell carcinomas and malignant melanoma — and of ocular cataracts and pterygia that would occur over the next four decades (Fraser *et al.* 1993). The calculation entailed, first, estimating the dose-response relationship between level of UVR exposure and the incidence from existing epidemiological data. Then, from knowledge of trends in ozone depletion and ground-level UVR during the

preceding decade, and from estimates of future trends in ozone damage, predictions were made of changes in ground-level UVR over coming decades. From these estimates, and appropriate amplification factors, the numbers of extra incident cases were predicted. The predictions for South Australia are shown in Fig. 1. (Note, however, that the techniques for making such predictions are still crude, and, in this particular case, there was inadequate allowance for minimal duration of exposure and for cancer latency periods. These predictions are therefore illustrative, not definitive!).

Increased UV-B exposure would also have deleterious effects on the world's biota, including impairing crop yields (Worrest & Grant 1989). The estimated danger to marine organisms could be significant, since increased UV-B irradiation of the ocean's surface could damage the photosynthetic phytoplankton population — the basis of the aquatic food chain (Smith *et al.* 1992). (A quarter of the protein supply in the human diet comes from the sea, as does much of the protein fed to livestock.)

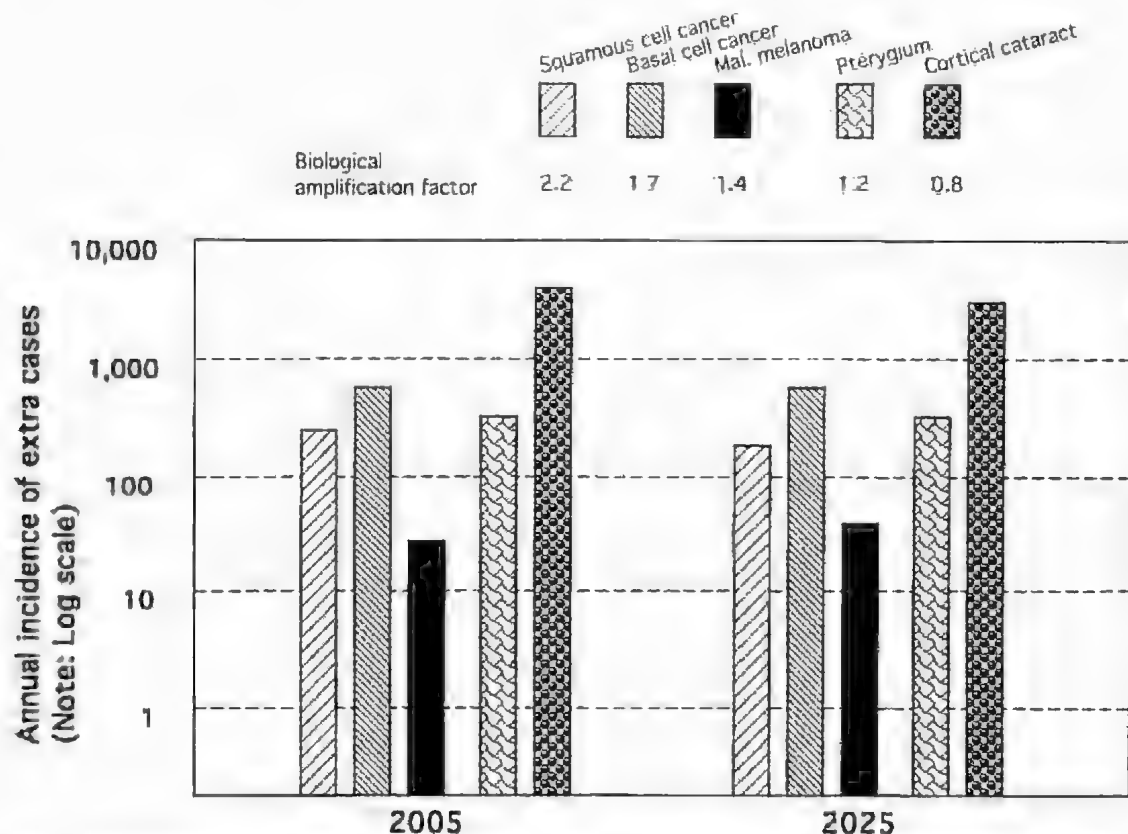


Fig. 1. Estimated annual extra numbers of cases of skin cancer and ocular lesions due to increased ground-level exposure to ultraviolet radiation, consequent upon stratospheric ozone depletion. Numbers are expressed relative to the (background) incidence of these conditions in 1990. (From: Fraser *et al.* 1993. Note also the caveats in the accompanying text.)

South Australia

Heathcote (1990) has proposed that climate change should not be considered in isolation from climate variability as the latter may provide valuable information on which to base estimates of change. An examination of the climate and ecology of South Australia provides particularly interesting perspectives of such variation with which to consider the possible human health effects of climate change.

Australia as a whole and South Australia in particular has one of the most variable climates on earth. This is no new phenomenon but has been the case for hundreds of thousands of years (Nicholls 1992; Cook 1992). This predictable but irregular variability has resulted in the adaptation of the flora and fauna of the State to suit such changeable conditions.

Covering one eighth of the Australian continent, South Australia lies wholly in the temperate zone. The land is low, with the inland areas being largely covered by plains, sand and gibber deserts. 80% of the State is less than 300 metres above sea level. The climatic consequence is that apart from the coastal areas, there are no significant mountain ranges to encourage precipitation evenly throughout the State. Much of SA, therefore, is arid or semi-arid (Gardner 1993).

Weather never replicates itself exactly from year to year (Voice *et al.* 1993). Australia has been found to have the highest interseasonal rainfall variability and runoff in the world (McMahon *et al.* 1987) with drought being a frequent occurrence when defined as annual rainfall in the lowest 10% of records (Gibbs & Maher 1967). SA is the driest State with four-fifths of the State normally receiving less than 250 mm of rain annually - while only one third of Australia as a whole receives less than 250 mm. The basic features of the SA climate are hot, dry summers with relatively mild nights and cool but not severe winters, where most of the rain falls between the months of May to August (Gardner 1993).

It is clear that changes to the rainfall pattern alone could dramatically alter the ecology of this State.

Not only is the geography of the land and natural fluctuations influential in climate variability in SA, but a phenomenon known as ENSO, or the El Niño Southern Oscillation plays a significant role in the climate of South Australia. The Southern Oscillation is a major shift in air pressure between Asia and eastern Pacific regions which effects changes to trade winds, cloud amounts and rainfall over the tropical Pacific through to Eastern Australia (Voice *et al.* 1993; Nicholls 1992), extending its influence as far west as the River Nile (Quinn 1992). The Southern Oscillation is measured by an index of the difference in air pressure between Tahiti and Darwin. A positive index (low pressure at Darwin) means that trade winds blowing strongly across the Pacific feed moisture into the

monsoons of Asia and Australia. A negative index (high pressure at Darwin) means that the trade winds are weak or even reversed.

A significant warming of the sea surface in the eastern equatorial Pacific occurring at the same time as negative index measurements of the Southern Oscillation, is known as El Niño. The reverse effect, known as La Niña, takes place when the Southern Oscillation index is positive and the waters of the eastern Pacific are cold. The combination of the Southern Oscillation and El Niño is known as the El Niño-Southern Oscillation or ENSO.

This is not a recent effect. Paleoclimatic records have uncovered evidence of the ENSO as far back as 1000 years (Cook 1992). It is predicted that ENSO is unlikely to change dramatically or vanish under conditions brought about by the level of climate change currently predicted (Voice *et al.* 1993). However, it is not yet known whether ENSO may become variable or more frequent, destabilising the present 12 month cycle.

At present, ENSO accounts for about 90% of major droughts in Eastern Australia. Further, this same phenomenon is responsible for approximately 20% of all rainfall variations in eastern Australia including flooding, wet seasons lasting six to nine months as well as less dramatic events (Voice *et al.* 1993). It is therefore a significant contributor to the extreme variability in the Australian, and South Australian, climate.

Over the past 200 years of white settlement, human activity in adapting and manipulating environments to provide for better living standards, may have increased human vulnerability to the effects of significant climatic and environmental variation (Heathcote 1990). In other words, human adaptation has been in the form of modifying the external environment as opposed to the longer evolution of native flora and fauna which modify their own physical characteristics and systems.

Human attempts at environmental modification in South Australia have included extensive land clearance resulting in desertification and increased salinity of soil and water. Deforestation of catchment areas has led to flooding and erosion, and agricultural practices have contaminated the land with pesticides and heavy metals. South Australia's only major river, the Murray, is heavily used as a water supply and irrigation base in the three States (New South Wales, Victoria and South Australia) through which it flows. In recent years, significantly lower water levels and reduced flow in this State, combined with pollution with phosphates and nitrates, have resulted in extensive algal blooms (Soong 1993). The Murray has a fall of only 20 metres across South Australia (Gardner 1993) and is therefore not a fast-flowing river, rendering it susceptible to algal blooms.

Within the context of such significant environmental degradation, attempts must be made to predict and prepare for human health needs in a climate change scenario where average global surface temperatures are predicted to rise by around 2–3°C by the year 2100 (IPCC 1992).

Over thousands of years of climatic variability, Australia's flora and fauna have evolved to accommodate the climate, and indeed to flourish. Nicholls (1992) describes adaptations in the behaviour and breeding patterns of the Red Kangaroo, the long-haired rat and other Australian birds, insects and plants. All have developed survival patterns of breeding in plague proportions in wet seasons when food is plentiful and a virtual shut down in times of extended drought.

More permanent increases in summer rainfall and higher minimum temperatures in SA as predicted by climate models (Heathcote 1990) could lead to plagues unhampered by the natural controls of drought and cold. In the past 12 months, excessive rainfall and milder than usual minimum temperatures have led to plagues of mice, locusts, various bird species, wasps and mosquitoes. Floods have created disaster and death in human populations. Water supplies have been contaminated with human and animal sewage (Walters 1993¹).

The human health consequences of such meteorological variation have included a South Australian outbreak of Ross River Virus (RRV) of epidemic proportions. There were in excess of 800 cases of RRV in the period mid-September 1992 to mid-May 1993 (Cameron 1993²). By comparison, previous lesser epidemics were in 1984, 136 cases and 1989, 115 cases (Weinstein 1991). The underlying annual mean number of cases over the last ten years (excluding epidemic years) is less than 10 cases per year (Bell *et al.* 1991). The 1992/93 epidemic occurred as a result of high rainfall and mild temperatures from August 1992 to February 1993 as reported by the South Australian Regional Office of the Bureau of Meteorology (1993) which provided perfect breeding conditions for mosquito vectors *Aedes vigilax* and *Culex annulirostris*.

Diseases predicted to increase include Murray Valley Encephalitis (MVE), also known as Australian encephalitis. Caused by a mosquito-borne *Flavivirus*, MVE was last recorded in South Australia in 1974. Excessive rains as a result of an ENSO event had led to an extended breeding season for the horon population, the natural reservoir of infection for MVE. The virus is transmitted via the mosquito vector *Aedes aegyptae* and has a case fatality rate from 0.3% to 60% (Benenson 1990) and is often around 30% (Manson-Bahr 1987). Nicholls (1986) subsequently devised a method, based on historical research, of predicting outbreaks of MVE using the Darwin mean air pressure of the Southern Oscillation.

Other predicted impacts of climate change in South Australia include the move south of dengue fever, tick borne diseases such as Lyme disease, and even malaria (Sutherst 1992³; Ewan *et al.* 1993). In February 1993, local transmission of falciparum malaria is reported to have occurred in Queensland, south of the nineteenth parallel (Murray-Smith & Weinstein 1993). Although Australia was certified free of endemic Malaria by the World Health Organisation in 1981, there are over 700 cases of imported Malaria annually. The common vectors for malaria, the *Anopheles farauti* s.l. and *An. punctulatus* mosquito are considered to exist only above the 19th parallel, known as Australia's malaria receptive zone. However, *An. farauti* is known to range south of the 21st parallel, while *An. annulipes*, previously implicated in local transmission of malaria in Victoria and New South Wales (Ford 1950), ranges as far south as Tasmania (Russel 1990).

The implication for South Australia is that with climatic change, at least *An. annulipes* is capable of establishing a niche here, becoming infected by biting cases which are at the gametocytic stage of the disease and transmitting the disease locally.

The spread of Lyme disease could occur because of increased vegetation due to higher rainfall in South Australia. Although no vector for the anaerobic spirochaetes of the Borrelia parasites, the causative agent for Lyme disease, has yet been identified in Australia (Russel *et al.* 1993), there is suggestive evidence from serology reports from patients with Lyme type symptoms, that indigenous Lyme borreliosis (LB) is widespread in Australia and that a number of strains of the disease are present (Barry *et al.* 1993⁴).

Perhaps more frequent mouse plagues would bring with them new and serious diseases such as the Hanta Virus which emerged in the US this year (Leduc *et al.* 1993; Mestel 1993). Methods of controlling such plagues are ad hoc at present, expensive (\$1.6m.) and largely inappropriate for long-term use. The use of poisons, such as strychnine in the 1993 South Australian mouse plague (Downward 1993⁵) is not a viable long-term response to problems that have their origins in ecological and climatic disruption.

¹WALTERS, R. (1993) Personal communication, State Water Laboratory, South Australia.

²CAMERON, S. (1993) Unpublished data. Communicable Diseases Control Unit, Epidemiology Branch, Public and Environmental Health Service, South Australian Health Commission.

³SUTHERST, R. W. (1992) The Likely Impact of Climate Change on Medical Vectors. Paper presented at the Australian Tropical Health and Nutrition Conference, Brisbane.

⁴BARRY, R. D., HUDSON, B. J., SHAPLIN, D. R. & WILLY, M. C. (1993) Evidence for an indigenous form of Lyme Borreliosis in Australia. Paper presented at the Australian Tropical Health and Nutrition Conference, Brisbane.

⁵DOWNWARD, R. (1993) Disaster management. Report to the 7th Standing Committee on Industry, Science, Technology, Transport, Communication and Infrastructure. Wikman, SA. Wed. 13th October.

Contamination of water supplies has led to anecdotal reports of increased incidence of diarrhoeal and gastrointestinal diseases. There have been 1250 cases of Hepatitis A or infectious Hepatitis in South Australia since 1983, with 510 of these occurring in 1986 (Bell *et al.* 1991). Hepatitis A is a disease of public health importance in flood situations or other disasters which affect infrastructure. Water-borne diseases such as giardiasis (caused by the protozoan *Giardia lamblia*), *Campylobacter jejuni* (found in milk, water, meat) and amoebiasis (*Entamoeba histolytica*) could also pose problems in a wetter SA, while increased temperatures may lead to more infection with *Legionella* and food borne disease such as *Salmonella* and *Yersinia*, the latter being already on the increase and of significant public health concern (Bell *et al.* 1991). *Legionella* bacteria survives better in water aerosol which contains blue-green algae (O'Brien & Bhopal 1993), this having significant implications for the transmission of the disease in a warmer climate scenario.

It is predicted that with global surface warming of 2-3°C the main direct hazard to health from a temperature increase comes from thermal extremes. South Australia endured temperatures in excess of 40°C in February 1993, provoking media headlines as far away as Brisbane of "Heatwave kills 36, hundreds in hospital" (The Courier Mail 1993), while in Adelaide it was "Heatwave drama as toll rises" (The Advertiser 1993). Children, the elderly and the unwell were the main groups affected.

Finally, SA currently enjoys up to 3,500 hours of sunshine annually, out of the approximately 4,380 hours possible (Gardner 1993). Increasing levels of UVR pose a worst case scenario of not only significantly increasing skin cancer rates, but also of initiating immunosuppression, rendering the population

more vulnerable to various infectious agents. Evidence from transplant patients, the immunocompromised and AIDS patients illustrate well the range of opportunistic infections which may result from sweeping population-based immunosuppression. The efficacy of immunisation may be reduced, and diseases which have been "controlled" in the past may therefore re-emerge.

Conclusion

One result of the increasing impact of *Homo sapiens* on the world's natural systems is that our focus of environmental health concern must move beyond the realm of polluted local environments and into the realm of disrupted natural systems. Anticipating effects on population health is made difficult by the combination of unfamiliarity, uncertainty and timing (the unacceptability of an empirical "wait-and-see" approach). The risks of cancer and cataracts from ozone depletion can be easily appreciated; likewise the health hazards from heatwaves. More difficult to conceptualise – but of potentially much greater impact are the anticipated indirect health consequences of climatic effects on food production and on the spread of infections, and, perhaps, immune suppression by ultraviolet radiation.

Some extreme, and extremely costly, technological adaptations may be possible – such as erecting ultraviolet barriers over living spaces or investing massively in seawater desalination. However, in general, human population health cannot be sustained if the Earth's natural systems are not maintained. For the first time in human history, there is evidence that various of these natural systems are becoming overloaded at a global level. This portends a frameshift in how we must think about "environmental health".

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**BIOLOGY OF PHYLACTEOPHAGA FROGGATTI RIEK
(HYMENOPTERA: PERGIDAE)
AND ITS PARASITOIDS IN SOUTH AUSTRALIA**

*By T. A. THUMLERT & A. D. AUSTIN**

Summary

Thumlert, T. A. & Austin, A. D. (1994) Biology of *Phylacteophaga froggatti* Riek (Hymenoptera: Pergidae) and its parasitoids in South Australia. Trans. R. Soc. S. Aust. 118(2), 99-113, 31 May, 1994.

Information is presented on the biology of *Phylacteophaga froggatti* Riek (the leaf-blister sawfly), an emerging pest of plantation and ornamental eucalypts in south-eastern Australia. The range of eucalypt species attacked, the extent of tree damage, seasonality, fecundity and longevity of *P. froggatti* are investigated for populations in the Adelaide region. The hymenopteran parasitoids associated with *P. froggatti* are reviewed. An illustrated key to the 17 species encountered in the Adelaide region is presented, along with notes on their biology, relationship with their host, and species recorded from other parts of Australia.

Key Words: *Phylacteophaga froggatti*, Pergidae, parasitoids, hyperparasitoids, Braconidae, Ichneumonidae, Chalcididae, Elasmidae, Encyrtidae, Eulophidae, Eupelmidae, Pteromalidae.

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by T. A. THUMBERT & A. D. AUSTIN^{*}

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Introduction

Phylacteophaga froggatti Riek, the leaf-blister sawfly, is a native leaf-mining species that is generally restricted in distribution to the south-eastern and south-western parts of the continent (Riek 1955; Benson 1963; Farrell & New 1980; Curry 1981). Larvae feed on a range of eucalypt species by mining the mesophyll layer between the upper and lower epidermis of large leaves. This pattern of feeding results in characteristic oval or elongate, brown blisters, which are most common on the lower branches of young trees (Farrell & New 1980; Nuttall 1985). Heavy infestations of *P. froggatti* cause substantial loss of photosynthetic area, resulting in stunted growth or death of trees. This damage is of most concern where large numbers of saplings exist in a confined area, such as eucalypt plantations, ornamental eucalypts in parks and gardens, and potted trees in outside nurseries.

In 1985 *P. froggatti* was accidentally introduced into New Zealand where it has become a serious pest of eucalypt forests and ornamental trees (Nuttall 1985; Kay 1986). This has led to the importation and release of two species of braconid wasp from Australia in an attempt to control this sawfly biologically (Austin & Faulds 1989; Faulds 1990).

Given the pest status of *P. froggatti*, relatively little work has been undertaken on its biology or that of its parasitoids. Other than the work of Farrell & New (1980), who provide a detailed account of some aspects of the biology of *P. froggatti* in the Melbourne area, the species has received only anecdotal attention (Froggatt 1899; anon. 1950; Riek 1955, 1970; Moore 1966; Curry 1981; Naumann 1983; Bungey 1986). Information on its parasitoids is even more limited.

Farrell & New (1980) record some observations on the development and mode of parasitism for two species, *Bracon* sp. and *Cirrospilus* sp. in the Melbourne area, while other workers have simply listed the species reared (Moore 1966; Curry 1981; Bouček 1988). In these studies no more than six species have been recorded and, with the exception of Bouček (1988), the accuracy of species identifications is questionable. More recently, Austin & Faulds (1989) have described two species of *Bracon* that have been introduced into New Zealand, while Faulds (1990) has reported the release and establishment of these species and discussed their potential for controlling *Phylacteophaga*.

The aim of the present study is to document more fully the biology of *P. froggatti*, focusing on aspects that have been largely neglected by previous workers. At the same time, detailed information is presented on the large parasitoid complex associated with *P. froggatti* in the Adelaide region. An illustrated key to their identification, as well as notes on their taxonomy, biology as either primary or hyperparasitoids, immature stages and seasonality are presented as a prelude to future studies on the ecology and possible control measures of this emerging eucalypt forest pest.

Materials and Methods

Field sites

Eucalypt trees infested with larvae and pupae of *P. froggatti* were monitored at several sites in the Adelaide region, viz., from the western coastal suburbs (Dover Gardens), city parklands and adjacent suburbs (Sturt), and Lobethal-Woodside area (Adelaide Hills), between August 1990 and July 1991. The first two sites comprise mostly ornamental trees (immatures of numerous species) in parks and along roadsides, while the latter site is semi-rural and comprises both ornamental trees

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and naturally growing trees in paddocks and along roadside verges (mostly *Eucalyptus camaldulensis*, *E. cladocalyx* and *E. leucosylen*). The climate of the first two sites is very similar with average monthly maximum and minimum temperatures of 23°C and 13°C, while the Lobethal-Woodside site has average monthly maxima and minima of 21°C and 8°C. The average annual rainfall for these two areas is substantially different (Adelaide 585mm; Lobethal 888mm).

Laboratory rearing

Infested branches, mostly of *E. camaldulensis*, were collected from the field, placed in plastic bags and returned to the laboratory. They were placed in containers of water at room temperature or constant 20°C and *P. froggatti* allowed to develop. Leaves with larvae, pupae and/or developing parasitoids were backlit with an optical fibre light to determine the exact stages present and observe their development. Most parasitised and unparasitised pupae were separated into 5 cm dia. plastic containers and allowed to complete development. Once emerge, adult *P. froggatti* and parasitoids were kept alive by supplying them with a smear of honey and water via a saturated cotton roll pushed through the lid of a small glass vial. Virgin female *P. froggatti* were sometimes isolated from males as soon as they emerged to provide individuals for laboratory experiments.

Fecundity and longevity

Virgin female *P. froggatti* which had emerged over a 24 hour period were held at constant 20°C with honey and water supplied. Ten individuals, randomly selected each day, were measured for body length, killed in 70% EtOH, squashed on a microscope slide and the number of fully developed eggs counted.

To determine the longevity of *P. froggatti*, adult females were kept in 20 cm diameter plastic cages and their survival monitored twice daily until all wasps had died. Longevity was compared for 1) virgin or mated females, 2) with or without water and honey, and 3) at five temperatures (10, 15, 20, 25, 30°C). Ten females that had emerged within a 12 hour period were randomly selected from stock cages and transferred into experimental containers. Three replicates were run for each of the above 20 treatments. Honey or water were not supplied during mating to those which went into the 'no food' treatments. All cages were held at 12:12 h photoperiod in temperature cabinets with $\pm 0.5^\circ\text{C}$ temperature ranges. The mean survival time for each treatment was calculated and plotted against temperature, and the regressions analysed using a 2-tailed F-test.

Taxonomy and scanning electron microscopy

Terminology for morphological structures generally follow Gauld (1984) and Gauld & Bolton (1988) for

ichneumonid and braconid wasps and Bouček (1988) for chalcidoids. Where necessary, morphological structures referred to in the key are indicated on the figures. Voucher material of all species have been lodged in the Waite Campus insect collection, University of Adelaide.

Specimens for SEM examination were killed and washed in a strong detergent solution before being dehydrated in 100% EtOH and critical point dried in an Emscope CPD 250. They were coated twice with carbon and gold/palladium before being examined under a Phillips 505 Scanning Electron Microscope.

Results and Observations

Taxonomy of Phylacteophaga

The taxonomy of *Phylacteophaga* species is confused and requires urgent study. Nominally, only one species, *P. eucalypti* Froggatt, is recognised which has been divided into four subspecies (*P. e. eucalypti*, *P. e. froggatti* Riek, *P. e. tasmanica* Riek and *P. e. occidentis* Benson) based on colour and size (Benson 1963). At least two of these subspecies (*P. e. froggatti* and *P. e. occidentis*) occur sympatrically and may therefore represent distinct biological species (Naumann 1983). However, of the several hundred specimens reared from leaf mines by us during 1990-91 all belong to the one colour form, that of *P. e. froggatti* Riek (i.e. antennal scape and pedicel and scutellum of female pale yellow to orange-yellow). Furthermore, mating of field-collected material in the laboratory was always successful, supporting the premise that either only one species is present or one is dominant in the Adelaide region. Because all recent authors (e.g. Farrell & New 1980; Curry 1981; Gaulds 1990) have adopted species level status for the subspecies *P. e. froggatti*, this approach will be used here to save confusion.

Mating

In the field, males were often observed perched on the dorsal surface of leaves with their body held at 45° above the surface, in the vicinity of ovipositing or resting females, or flying in small swarms of 5-10 individuals, close to leaves where mating pairs were perched. Copulation is strophandous, i.e. male and female are joined end-to-end with the male genitalia twisted through 180° (Gauld & Bolton 1988). In the laboratory mating took 2-3 minutes. During copulation the female stands with her wings folded at rest, while males have their wings spread at about 45° and periodically fan them. After uncoupling, the female immediately moves away and the male remains in place, tapping its abdomen several times on the leaf surface before flying off.

Fecundity and oviposition

The number of eggs carried by virgin females ranged from 57 to 87, while egg number within these limits was positively correlated with both age and size of females ($r = 0.76$ and $r = 0.66$, $P < 0.05$). On landing, female *P. froggatti* move sideways over the surface of a leaf perpendicular to the mid vein, with this movement continuing until an oviposition site is chosen. The female saws into the leaf tissue for 5-10 sec. then remains stationary for 3-4 min while ovipositing. At this time the body and antennae are held at an angle of about 45° to the leaf and to the mid vein, possibly to position the egg so that the larva hatches in the direction towards the apex of the leaf. Once completed, the female rubs her abdomen over the position of the egg spot three or four times, possibly to seal the hole, and then moves away, either staying on the same leaf or moving to another leaf to oviposit. Eggs are generally laid close to the mid vein and along the length of the leaf, but not in the distal 20-30 mm. The small egg spots, about 0.8 mm in diameter, form raised globulous structures (egg-galls) on the surface of the leaf. The number of egg spots per leaf ranged from 7-170, with numbers over about 90 representing the ovipositions of more than one female.

Life-history stages

The morphology, colour and size of the egg, larval instars and pupa of *P. froggatti* are virtually identical to those described by Farrell & New (1980). Briefly, the egg is flattened and oval in shape, measuring 0.75×0.5 mm. There are five larval instars in the female and four in males. For the Adelaide population females had mean head capsule widths of 0.49 (I), 0.62 (II), 0.80 (III), 1.01 (IV) and 1.25 mm (V) ($n \geq 25$ in each case), with males being virtually identical to female instars I-IV. These sizes are almost identical to those measured for the Melbourne population by Farrell & New (1980), with the exception of female instar V which averaged 1.08 mm in the latter study. This discrepancy may be due to our selection of larvae from non-overlapping mines, where there was no competition for food between individuals. At room temperature in the laboratory during January and February (daily average about 23°C) larval development to cocoon initiation (i.e. including the prepupal period) took 15-18 days and the complete life-cycle about 30-35 days.

Pupation is preceded by a prepupal stage, distinguished from the last larval instar by a lighter-coloured head capsule. The prepupa moves away from the light perimeters of the mine into a more central position where it begins to spin a thin ovoid cocoon. Silk is laid down from mandibular glands as it swings its head from side to side. The cocoon is attached to the mine floor and the leaf surface above by silk, and forms an annulus of creases in the blister tissue. The

period from cocoon initiation to adult emergence took about eight days in the laboratory for both sexes. Two to three days after cocoon formation the prepupal cuticle was shed revealing the eye spots and appendages of the developing pupa. By the fifth day the pupa became pigmented, at which stage the sex of individuals could be determined by the colour of the thorax and presence of the female ovipositor, the thorax of males being black and that of females orange. The pupa moulted on day seven into the preadult stage, which is characterised by having all the features of a fully formed adult. The body is completely pigmented and the wings, which begin to unfold, are frequently fanned within the mine to help them dry. On the eighth day an oval-shaped hole is cut in the top of the mine, and the wasp voids a green-grey meconium just before exiting or immediately afterwards. In the laboratory approximately 25% of adults died after failing to emerge from their mine. This mortality was highest for leaves containing multiple individuals.

Longevity and overwintering

To determine the optimal holding conditions for *P. froggatti* in the laboratory and determine the potential for the species to overwinter as adults, longevity of wasps was measured at various temperatures and combinations of mated or unmated females, with food and water supplied or not. The regressions of mean survival time against temperature were significant for the four combinations of virgin and mated females, with and without food and water supplied (Fig. 1). The slope of the regression for females with food was significantly different from those without food and water for both virgin ($F = 6.85$; d.f. = 2, 6; $P < 0.05$

Fig. 1a) and mated females ($F = 4.74$; d.f. = 2, 5; $P < 0.05$ - Fig. 1b), but mating did not affect the survival of the females for either of the treatments with ($F = 4.5$; d.f. = 2, 5; $P > 0.05$) or without food and water ($F = 1.64$; d.f. = 2, 6; $P > 0.05$). In Figure 1b the data for mated females with food and water supplied at 10°C are excluded because of the breakdown of the temperature cabinet part way through the experiment. The longevity of females was increased when held at lower temperatures and when water and honey were supplied, but was not affected by mating. It is not known whether both water and honey were responsible for the increase in the survival rate of the females, as these factors were not tested separately. Possibly only water is required to prevent females from desiccating, and food is unimportant for longevity, though it may be necessary for increased fecundity.

The longest that adult females survived in the laboratory at temperatures below 10°C was 28 days. Hence, it seems unlikely that *P. froggatti* overwinters only as adults. A small number of occupied mines was found on trees in coastal suburbs of Adelaide during June and July, but at no other sites. It seems likely,

therefore, that some pupae continue developing in refuge areas until about mid winter and the subsequent adults remain quiescent for the rest of winter before ovipositing into leaves in late August or early September (see Fig. 2).

Mine development

First and 2nd instar larvae first mine towards the distal end of the leaf following the direction of the venation, but as they grow with each subsequent moult, the mine becomes progressively larger and circular or oval in shape. As observed by previous authors (Farrell & New 1980; Nuttall 1985; Kay 1986), mines generally follow along the mid-vein of the leaf and, when more than one larva is present, their mines often merge so that almost the whole leaf can become blotched. The largest number of larvae observed to complete development on a single large leaf was 21, so that any remaining eggs from the large numbers of ovipositions (see above) either died beforehand or were eaten by the first emerged larvae. Leaves supporting more than about 10 larvae often resulted in smaller adult wasps compared with leaves supporting fewer larvae. Other authors (Farrell & New 1980; Curry 1981) have reported *Phylacteophaga* as confining its development only to the top surface of a leaf. This was confirmed here for eucalypt species that have differently textured

dorsal and ventral surfaces, but for species with isolateral leaves (i.e. identical surfaces on leaves hanging vertically), mining was carried out on either side, sometimes resulting in individual larvae being separated only by the internal venation of the leaf.

Damage in trees

The levels of damage varied between infested trees and between individual sites, possibly because of differences in the tree species present, their size, age and health. Quantifying damage for these variables was beyond the scope of this study but casual observations in the field allow for some useful generalisations to be made. Trees which supported large numbers of *P. fraggattii* mines were similar in several respects: they were usually small (<4 m tall), were often situated on roadsides, carparks, parklands or isolated groups in paddocks, and were usually sheltered to some degree from westerly winds. Possibly sheltered localities prevent adult wasps from being blown away from their host plant, since they are not strong fliers. Trees that became heavily damaged appeared healthy in the early stages of attack, in that they had dense lush foliage and did not appear to be stressed. As reported by Farrell & New (1980), damage is more severe towards the base of trees, particularly on low hanging branches. The apex region is usually not attacked, especially for trees above 4.5 m in height. In some suburban areas, where there were many young trees of the same species (1–2 m in height), damage often reached very high levels, causing leaf shedding and sometimes death of saplings. Well-established trees (>8 m high), were far less frequently attacked and, if so, were usually in close proximity to heavily infested young trees. Mines on such trees were generally confined to low hanging branches with semi-mature leaves.

Host range

The range of tree species attacked by *Phylacteophaga* spp. was compiled by reviewing previous studies, as well as surveying a wide range of trees in the Adelaide region during 1990–91. Trees in open situations, nurseries and gardens were examined, with those in the latter two areas being used to confirm species identification. The data presented in Table 1 show that at least 27 eucalypt species are susceptible to attack both in Australia and New Zealand, with most of these records being attributable to *P. fraggattii*. In Australia the most widely infested species are *Eucalyptus botryoides*, *E. camaldulensis*, *E. citriodora*, *E. cladocalyx*, *E. ficifolia*, *E. globulus* and *E. grandis*. Also, several non-eucalypt species have been reported as hosts, but there is some doubt as to the accuracy of at least some of these accounts as they have mostly not been confirmed since the initial reports.

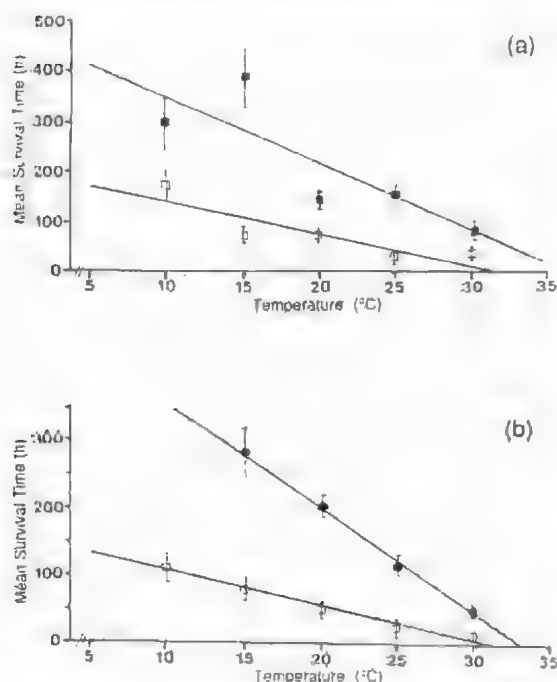


Fig. 1. Longevity of ♀ *Phylacteophaga fraggattii* measured as the mean survival time for three replicates of 10 wasps (\pm S.E.) at different temperatures: (a) for virgin ♀♀ with food and water supplied (■) and without food and water (□); and (b) for mated ♀♀ with food and water supplied (●) and without food and water (○).

Parasitoid species

Over the period of this study 17 species of hymenopteran parasitoids were associated with *P. froggatti*. A list of these species and summary of their biology is presented in Table 2, and a key to their identification given in the Appendix. Eleven species were primary parasitoids of either the larval or pupal stages. Three were confirmed as facultative hyperparasitoids (*Elasmus australiensis* Girault, *Cirrospilus margiscutellum* (Girault) and *Eupelmus* sp.), while three have not had their biology conformed (*Lariophagus* sp., *Pediobius* sp. and *Chrysonotomyia* sp. 2). The species in this latter group were not positively reared from *P. froggatti*, but rather emerged into rearing containers with eucalypt leaves infested with host larvae. There is a possibility that these species had come from other leaf mining hosts, though none of the latter was seen after careful inspection of the

leaves. It is likely, therefore, that these three species are parasitoids of *P. froggatti*, but further study is required to confirm this.

Seasonality of *Phylacteophaga froggatti* and its parasitoids

Fortnightly field excursions from August 1990 to July 1991 to collect *P. froggatti* and parasitoids were used to determine the approximate seasonality of the species involved in the Adelaide region. Egg spots and early mine initiation were first evident on trees in the Adelaide Plains in late August 1990 and pupae and preadult stages in mines were present up until late May 1991. A few occupied mines were found in June and July on several trees, only in the western (coastal) suburban areas. Although relative abundance of species was not determined, it was clear from the number of infested leaves and trees that *P. froggatti* is most

TABLE 1. List of tree species which have been recorded in the literature and during this study as susceptible to damage by *Phylacteophaga* spp. (sources of information are as follows: 1, Anon. [1950] and 2, Moore [1966], coastal N.S.W.; 3, Riek [1955] and 4, Farrell & New [1980], Melbourne region, Vic.; 5, this project [1990-91], Adelaide region, S.A.; 6, Curry [1981], Perth region, W.A.; 7, Nuttall [1985] and 8, Kay [1986], New Zealand; sources 3-5, 7 and 8 are for *Phylacteophaga froggatti*).

Host Plant	Recorded <i>Phylacteophaga</i> damage							
	N.S.W.		Vic.		S.A.	W.A.	N.Z.	
	1	2	3	4	5	6	7	8
<i>Eucalyptus botryoides</i>	✓	✓		✓		✓	✓	✓
<i>E. camaldulensis</i>	✓				✓	✓	✓	
<i>E. cinerea</i>					✓	✓	✓	✓
<i>E. citriodora</i>		✓			✓	✓	✓	
<i>E. cladocalyx</i>	✓	✓			✓	✓		
<i>E. diversicolor</i>						✓		
<i>E. ficifolia</i>	✓	✓				✓	✓	
<i>E. globulus</i>	✓	✓	✓			✓	✓	
<i>E. gomphocephala</i>						✓		
<i>E. grandis</i>			✓			✓		
<i>E. lehmannii</i>						✓		
<i>E. leucosylon</i>							✓	
<i>E. leucosylon rosea</i>					✓			
<i>E. longifolia</i>					✓			
<i>E. maculata</i>		✓						
<i>E. macarthurii</i>							✓	
<i>E. marginata</i>						✓		
<i>E. melliodora</i>						✓		
<i>E. nichesii</i>							✓	
<i>E. ovata</i>							✓	
<i>E. perrintana</i>		✓					✓	✓
<i>E. punctata</i>					✓			
<i>E. robusta</i>		✓				✓		
<i>E. rudis</i>					✓	✓		
<i>E. saligna</i>							✓	✓
<i>E. sideroxylon</i>		✓					✓	
<i>E. viminalis</i>							✓	
<i>Agonis flexuosa</i>								✓
<i>Betula</i> (Birch)								✓
<i>Lophostemon confertus</i> (Tristania)	✓			✓				✓
<i>Quercus palustris</i>							✓	
<i>Q. robur</i>							✓	

Species of Parasitoid	Family	Stage of <i>P. froggatti</i> attacked	Solitary (S) or Gregarious (G)	Endoparasitoid (N) or Ectoparasitoid (C)	Primary (P) or Hyperparasitoid (H)
<i>Bracon confusus</i>	Braconidae	larva; pupa	S	C	P
<i>Bracon phylacteophagus</i>	Braconidae	larva; pupa	S	C	P
<i>Paraphylax</i> sp.	Ichneumonidae	pupa	S	C	P
<i>Brachymeria</i> sp.	Chalcididae	pupa	S	N	P
<i>Elasmus australiensis</i>	Elasmidae	?pupa	S	C	P; H
<i>Apleurotropis</i> sp.	Eulophidae	larva	G	?N	P
<i>Chrysonotomyia</i> sp. 1	Eulophidae	larva	G	C	P
<i>Chrysonotomyia</i> sp. 2	Eulophidae	—	—	—	—
<i>Cirrospilus margiscutellum</i>	Eulophidae	larva; pupa; pa	S	C	P; H
<i>Cirrospilus occipitis</i>	Eulophidae	pupa	S	C	P
<i>Cirrospilus</i> sp. 3	Eulophidae	larva	S; G	C	P
<i>Cirrospilus</i> sp. 4	Eulophidae	—	S	C	P
<i>Cirrospilus</i> sp. 5	Eulophidae	pupa	S	C	P
<i>Diaulomorpha</i> sp.	Eulophidae	larva; pupa	G	C	P
<i>Pediobius</i> sp.	Eulophidae	—	—	—	—
<i>Eupelmus</i> sp.	Eupelmidae	pupa	S	C	P; H
<i>Lariophagus</i> sp.	Pteromalidae	—	—	—	—

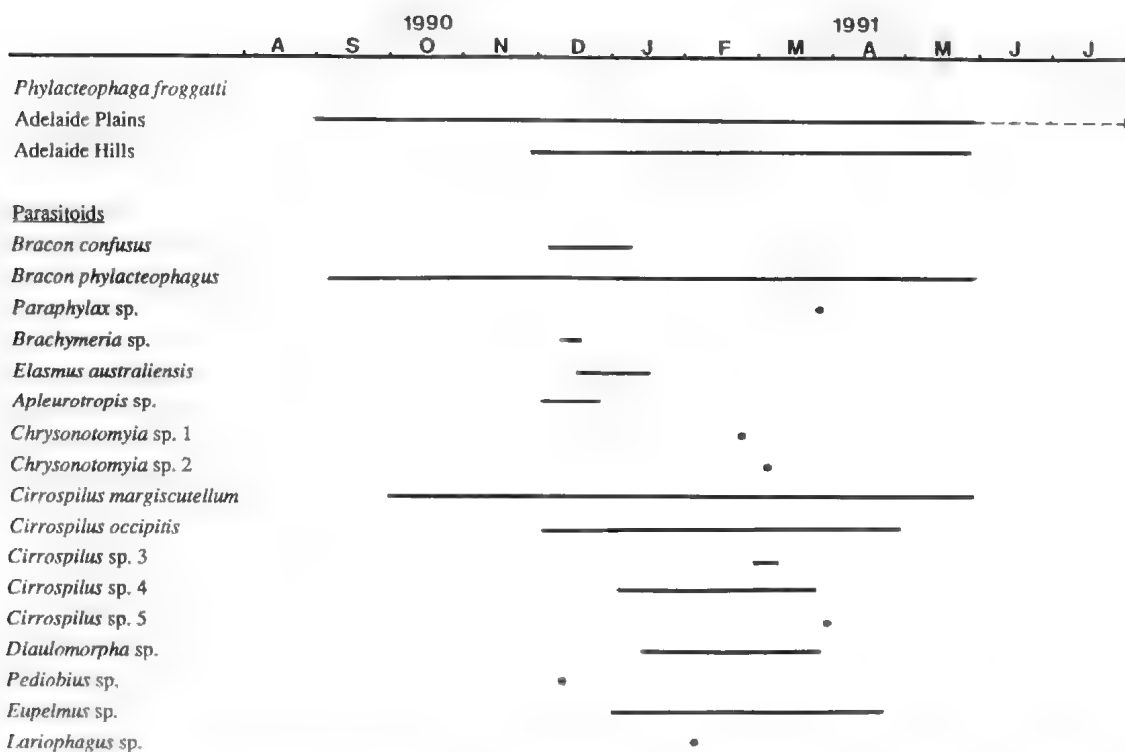


Fig. 2. Seasonality of *Phylacteophaga froggatti* and its parasitoids in the Adelaide region for 1990-91, determined by the presence of larvae and pupae in leafmines.

numerous at sites on the Adelaide Plains from about early December to late March (Fig. 2), and that there are three, possibly four, peaks in numbers over the period September to March. In the Lobethal-Woodside area (Adelaide Hills), largest numbers occurred slightly later, from about early January to late March, with egg spots and mine initiation not appearing until later November, presumably because of the cooler average temperatures there compared with the Adelaide Plains.

Of the 17 species of parasitoids, six were encountered over a period of two months or more (i.e. *Bracon phylacteophagus* Austin, *Cirrospilus margiscutellum*, *C. occipitis* Girault and *Cirrospilus* sp. 4, *Eupelmus* sp. and *Dialomorpha* sp.) (Fig. 2), and of these (in descending order) *C. margiscutellum*, *B. phylacteophagus*, *Eupelmus* sp. and *Dialomorpha* sp. were reared in the largest numbers. No parasitised hosts or parasitoid pupae were found in mines during July and August, though two adult female *B. phylacteophagus* and one *C. margiscutellum* were located in old mines during this time, indicating that these and possibly all parasitoids in the *P. froggatti* complex overwinter quiescently as adults.

Levels of parasitism

Collections of mined larvae during January and February 1991 enabled assessment to be made of the levels of parasitism in the field at three separate sites, viz., Lobethal (Adelaide Hills), Sturt and Dover Gardens (Adelaide Plains) (Table 3). These data show a large range in the level of parasitism of *P. froggatti* (15.6 to 60.3%), and in all cases *C. margiscutellum* was by far the most important parasitoid. Other parasitoids contributed 0 to 11.5% of total parasitism, of which *B. phylacteophagus* was most common. These data, however, represent a minimum estimate of percentage parasitism, particularly for the Sturt sample, where *P. froggatti* were mostly represented by early life-history stages when collected, so that those sampled could have been parasitised if left in the field. Because *C. margiscutellum* is capable of paralysing and feeding on all stages of *P. froggatti* from early instars to the preadult stage, an estimate of the maximum potential parasitism was obtained by adding the measured level of parasitism with the proportion of hosts still viable.

Biology of parasitoid species

Family Ichneumonidae

Paraphylax sp.

FIG. 5

There are more than 50 recognised species of *Paraphylax* from Australia, the majority of which are undescribed (Gauld 1984). Where their biology is known, they have been recorded mostly as primary

ectoparasitoids and hyperparasitoids of lepidopteran hosts. The single male specimen reared here in March 1991 is an ectoparasitoid of *P. froggatti* larvae. It belongs to the *covax* species-group, and is probably the same species as that recorded by Gauld (1984) from *P. froggatti* in south-eastern Australia. Being the only ichneumonid in this parasitoid complex, *Paraphylax* sp. can be easily identified by its characteristic wing venation.

Family Braconidae

Bracon confusus Austin & *B. phylacteophagus* Austin

FIGS 3, 4, 6

Both these species are solitary primary ectoparasitoids of third instar larvae to early stage pupae of *P. froggatti* (Table 2). *B. phylacteophagus* was the more commonly encountered species of the two, and was found associated with its host for the same period that occupied mines were present in the field (September to May). *B. confusus* was collected for only a short period during December-January. The biology of these species has been discussed by Austin & Paulds (1989) and Paulds (1990) and only observations complementary to those given by these authors are presented here. Prior to 1989, references to *Bracon* associated with *Phylacteophaga* did not recognise the presence of two sympatrically occurring species.

B. confusus and *B. phylacteophagus* oviposit one egg, rarely two, in a mine, either next to or onto the surface of the host. The host larva is paralysed at oviposition, thereby allowing the secure attachment of a newly emerged *Bracon* larva in the absence of an active host which normally whips its abdomen about when disturbed. Late stage *Bracon* larvae are easily distinguished from other parasitoids by their large size, dorsal ampullae and covering of long hairs, but they are identical to each other. Contrary to the findings of Farrell & New (1980), most larvae which we gently dislodged from a host with a fine brush did not die, but rather successfully reattached themselves. When feeding is completed, *Bracon* larvae normally move away from their host before commencing cocoon construction but occasionally pupate inside their host's pupal cocoon. When spun away from a host pupa, *Bracon* cocoons often have loose frass and moulted cuticles incorporated into their silk matrix. They are white in colour, ovoid in shape and measure about 7.0 × 1.3 mm. The confined prepupa deposits a meconium at one end of its cocoon and then bunches into the opposite end so that it occupies only about half of the internal space. Adults emerged in the laboratory 11-12 days after the commencement of cocoon construction. Adult *B. phylacteophagus* held at constant 15°C were still alive after 68 days and individuals were observed to feed on the honey and water provided.

Along with *Paraphylax* sp., *B. confusus* and *B. phylacteophagus* can be easily recognised by their relatively complete venation and large size (<3 mm), and the species separated by their colour and differences in pilosity.

Family Chalcididae

Brachymeria sp.

FIG. 7

This genus is a moderately large genus in Australia comprising primary parasitoids and obligatory hyperparasitoids of the pupae of a great range of holometabolous insects, but particularly Lepidoptera (Bouček 1988). The species recorded here was reared from several pupae of *P. froggatti* during one week in December 1990. *Brachymeria* sp. is easily identified by its small robust form, enlarged hind femur, elongate postmarginal vein, and densely punctate dorsal mesosoma.

Family Eupelmidae

Eupelmus sp.

FIG. 8

This species was generally reared as a solitary primary parasitoid from the pupal stage of its host, but on several occasions was also found to be hyperparasitic on smaller conspecific larvae and those of several other unidentified parasitoids. Mature larvae can be identified from the other common parasitoids in mines by the presence of dorsal ampullae and dense, long hairs on the thoracic segments. *Eupelmus* sp. was reared from *P. froggatti* from mid summer to mid autumn. Adults can be separated from the other species in the complex by the presence of a greatly enlarged mesopleuron, exposed ovipositor, and form of the wing venation.

Family Elasmidae

Elasmus australiensis Girault

FIG. 9

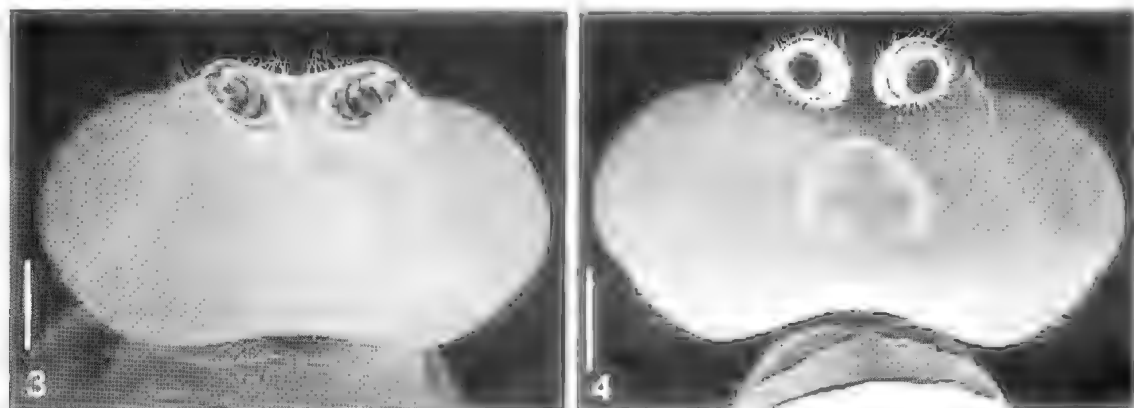
This species was reared either as a solitary primary ectoparasitoid or hyperparasitoid of *P. froggatti* during December and January. Previous reports (Riek 1967; Austin & Allen 1989; Allen 1990) have recorded this species as being gregariously hyperparasitic on ichneumonid pupae associated with the lepidopteran defoliator *Uraba lugens* Walker. It can be readily identified by its large disc-shaped hind coxa, cream coloured legs with black hairs and spines, and distinctive criss-cross pattern of black hairs on the hind tibia. See Riek (1967) for additional taxonomic information and list of synonyms.

Family Pteromalidae

Lariophagus sp.

FIGS 10, 11

According to Bouček (1988), this small genus is represented in Australia only by *L. distinguendus* (Foerster), a cosmopolitan parasitoid of beetles associated with stored grain. The single specimen reared here was removed in early February 1991 from a *P. froggatti* mine that did not contain any other parasitoids or other potential hosts. Given the paucity of biological information available on this genus we are unable to speculate further on this species. However, given that a dead *P. froggatti* larva was the only other occupant of the mine, we have assumed that *Lariophagus* sp. is either a primary or hyperparasitoid on it. This small nondescript species is the only pteromalid in the parasitoid complex and it can be best identified by the presence of five tarsal segments and six funicle segments of the antenna.



Figs 3, 4. Dorsal view of the head of ♀ *Bracon* spp.: 3, *Bracon phylacteophagus* Austin, 4, *Bracon confusus* Austin. Scales = 250 µm.

Family Eulophidae

Pediobius sp.

FIG. 12

Members of this genus are known to be primary and hyperparasitoids of eggs, pupae and sometimes larvae of various insects, mainly of Lepidoptera, Coleoptera, Diptera and other Hymenoptera, with several species being reported as attacking leaf-miners (Bouček 1988). An unidentified *Pediobius* species is hyperparasitic on *U. lugens* (Austin & Allen 1989; Allen 1990), the latter occasionally appearing on the same host plants as *P. froggatti*. However, variation in sculpturing on the scutellum indicates that the *Pediobius* associated with these two hosts are different species. Previously, *P. bruchicida* (Rondani), a gregarious species (Bouček 1988), has been found as a hyperparasitoid on *B. phylacteophagus* in New Zealand (Faulds 1990), and this species resembles closely the single specimen recorded here. *Pediobius* sp. was reared in a container from a number of leaves mined in late December 1990. Inspection of these leaves revealed the presence of no other potential hosts. Like *Apleurotropis* sp. and *Diallomorpha* sp., this species can be identified from others in the complex by the presence of several long hairs on the scutum and scutellum, and the posterior expansion of the scutellum. In addition to the characters in the key, it can be separated from *Apleurotropis* sp. by the absence of a postero-medial sulcus on the scutum and from *Diallomorpha* sp. by the very distinctive colour of the latter species.

Apleurotropis sp.

FIG. 13

This genus has previously been recorded as emerging from *P. froggatti* mines (Rick 1955; Farrell & New 1980), with Bouček (1988) listing *A. unnotipennis* (Girault) as parasitising *P. eucalypti* in the Melbourne area. Material reared over a three week period in December 1990 here confirms that this species is gregarious, with the larvae probably being endoparasitic, as holes were found in the body of the host next to the parasitoid pupae. A single mine of a late stage *P. froggatti* larva was found to contain 12 parasitoid larvae and pupae, of which most completed development in the laboratory. Compared with *Pediobius* sp., this species can be easily recognised by the presence of a large postero-medial sulcus on the scutum (see above).

Diallomorpha sp.

FIGS 14, 15

This gregarious primary ectoparasitoid attacks the larvae and pupae of *P. froggatti*, with up to 10 parasitoids being recorded from a single mine. At room

temperature most individuals in a single mine emerged within 13 days after the commencement of pupation. Mature larvae can be easily recognised from the other common parasitoids in the complex because of their gregarious behaviour and absence of dorsal ampullae. Adults can be recognised by their metallic green-gold colour, white legs and light brown antennae (see comments under *Pediobius* sp.). An apparently undescribed species belonging to this genus has been recorded from *Phylacteophaga* mines in Western Australia and elsewhere in Australia (Bouček 1988), and this may be the same species as reared here.

Chrysonotomyia sp. 1 and sp. 2

FIGS 16, 17

According to Bouček (1988), members of this medium-sized genus of about 40 described Australian species, develop in the eggs or young larvae of leaf-mining and gall-forming Diptera and Lepidoptera. Virtually no biological information is available for any Australian species, except for one reared from *Perthida glyphopa* Common (jarrah leaf-miner) in the warmer regions of the Darling Ranges and coastal regions of south-west Western Australia (Mazanec 1988). It is a solitary endoparasitoid most frequently of the 2nd and 3rd instar larvae.

Two species belonging to this genus have been associated with *P. froggatti* in the Adelaide region. *Chrysonotomyia* sp. 1 was reared as a gregarious primary ectoparasitoid of a single late stage larva of *P. froggatti* collected at Lobethal in March 1991, while two specimens of *Chrysonotomyia* sp. 2 were reared only from mined leaves in February 1991 collected at the Dover Gardens site, and therefore are only tentatively assumed to be parasitic on this host. Although very small in size (about 1 mm in length), these two species can be separated from the other eulophid genera in the complex by the antennal funicle being only 2-segmented and the scutellum lacking a submedial groove. They can be separated from each other by the form of the wing venation and their colour.

Cirrospilus margiscutellum (Girault)

FIGS 18, 19, 22

Cirrospilus is a large and taxonomically difficult genus of small often brightly patterned wasps which are well-known primary and hyperparasitoids of eucalypt leaf-mining insects. Two described species have previously been reared from *Phylacteophaga* spp., viz., *C. margiscutellum* (Girault) from Western Australia and *C. occipitis* Girault from N.S.W. (Bouček 1988), while undetermined species have been reared from *P. froggatti* in Melbourne by Rick (1955) and Farrell & New (1980) and in Western Australia by

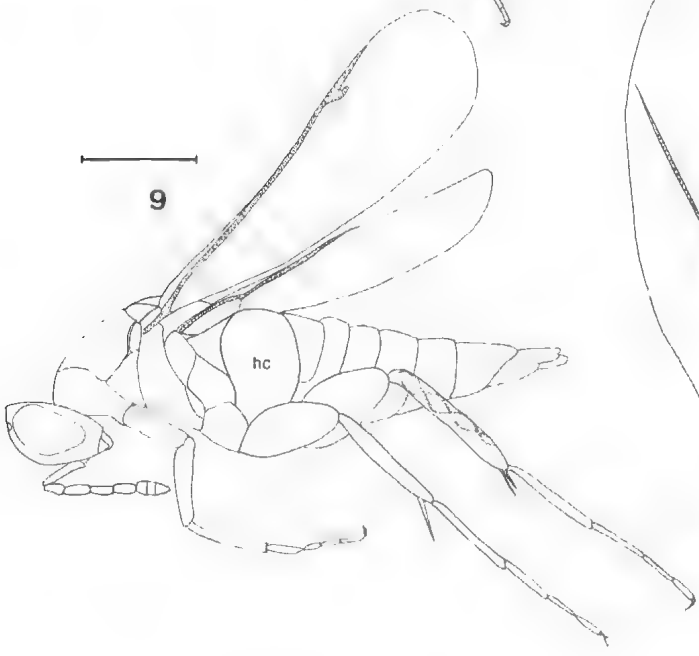
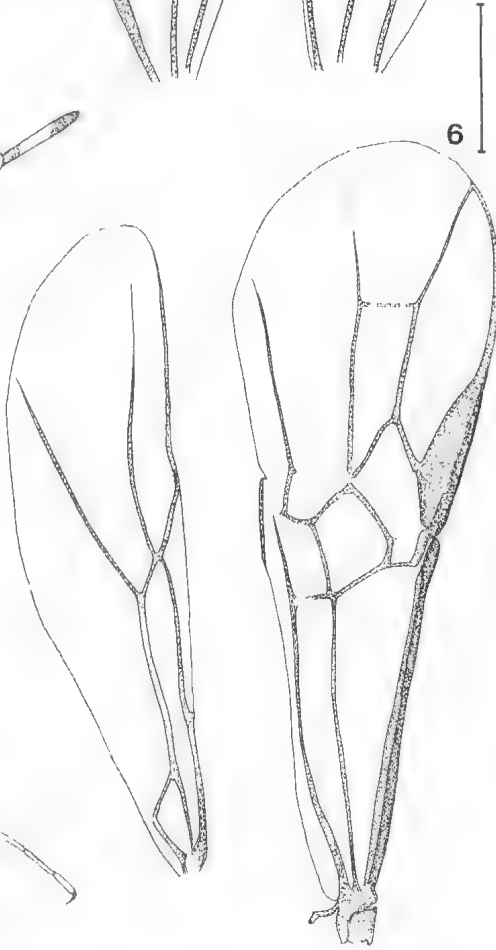
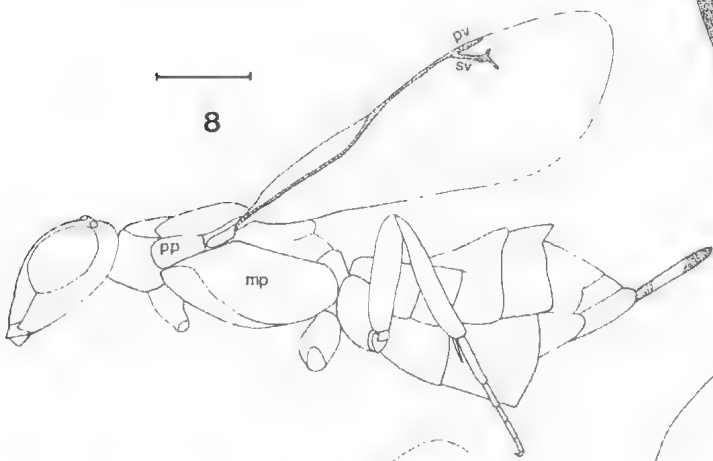
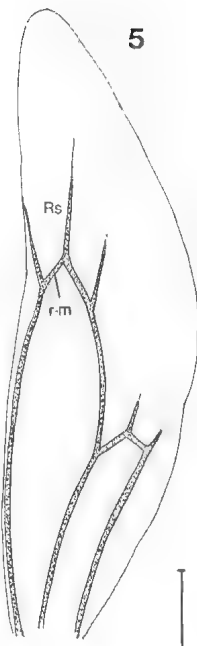
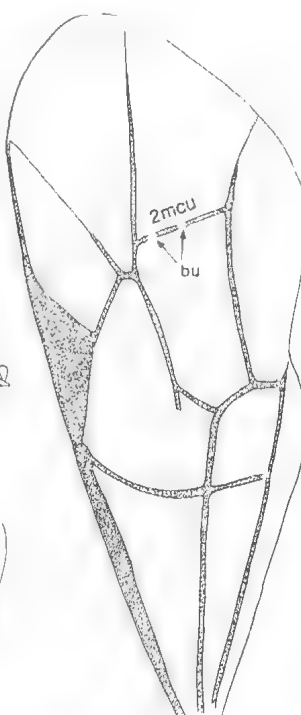
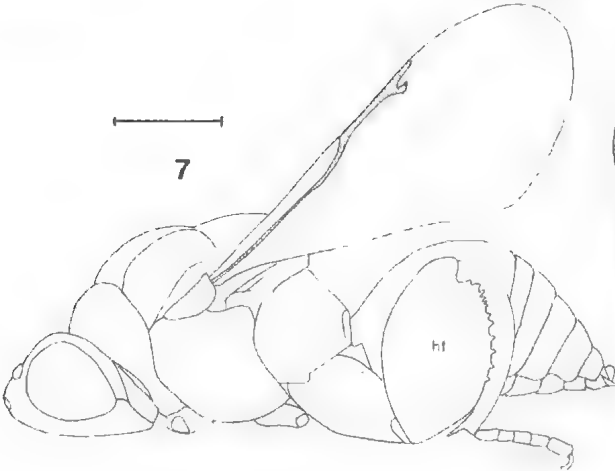


TABLE 3. Mortality of *Phylactoeophaga froggatti* as revealed by collections made during January and February 1991, from Lobethal where trees were in relatively early stages of attack, and from Sturt and Dover Gardens where trees had been heavily attacked during the preceeding weeks (— = information unavailable).

	Collection Sites		
	Lobethal	Sturt	Dover Gardens
Total number of mines examined	434	899	410
% already emerged	45.6	0	1.2
Viable <i>P. froggatti</i>			
% larvae, pupae & preadults	13.8	79.6	6.3
Cause of Death Unknown			
% larvae and pupae	10.1	—	—
% preadults	10.6	—	—
% Total	20.7	3.8	21.0
Parasitism			
% parasitized by			
<i>Cirrospilus margiscutellum</i>	13.8	15.5	60.7
% parasitized by <i>Bracon</i> spp.	1.6	0	0
% parasitized by others	0.2	1.1	0
% Total parasitism	15.6	16.6	60.7
% max. potential parasitism	29.4	96.2	67.0

Curry (1981). Clearly, at least some *Cirrospilus* spp. are widespread in Australia. Here we record *C. margiscutellum* from the Adelaide region and *C. occipitis* from Perth (material in ANIC) for the first time, indicating that these species are distributed across the southern part of the continent, at least.

C. margiscutellum was by far the most commonly reared parasitoid associated with *P. froggatti* in the Adelaide region (Table 3), and was present in mines for nearly the whole time that host larvae and pupae were available (late September to late May). As shown by Farrell & New (1980), laboratory observations confirm it to develop as a solitary primary parasitoid of third instar larvae to late stage pupae, as well being hyperparasitic, in the Adelaide region, on the larvae of *Bracon* spp., *Eupelmus* sp., *Diadromorpha* sp. and small conspecific larvae occurring in the host mine. When multiple *P. froggatti* were found in mines, with some parasitised by *Bracon* spp., the latter appeared to be preferentially parasitised by *C. margiscutellum* rather than unparasitised primary hosts.

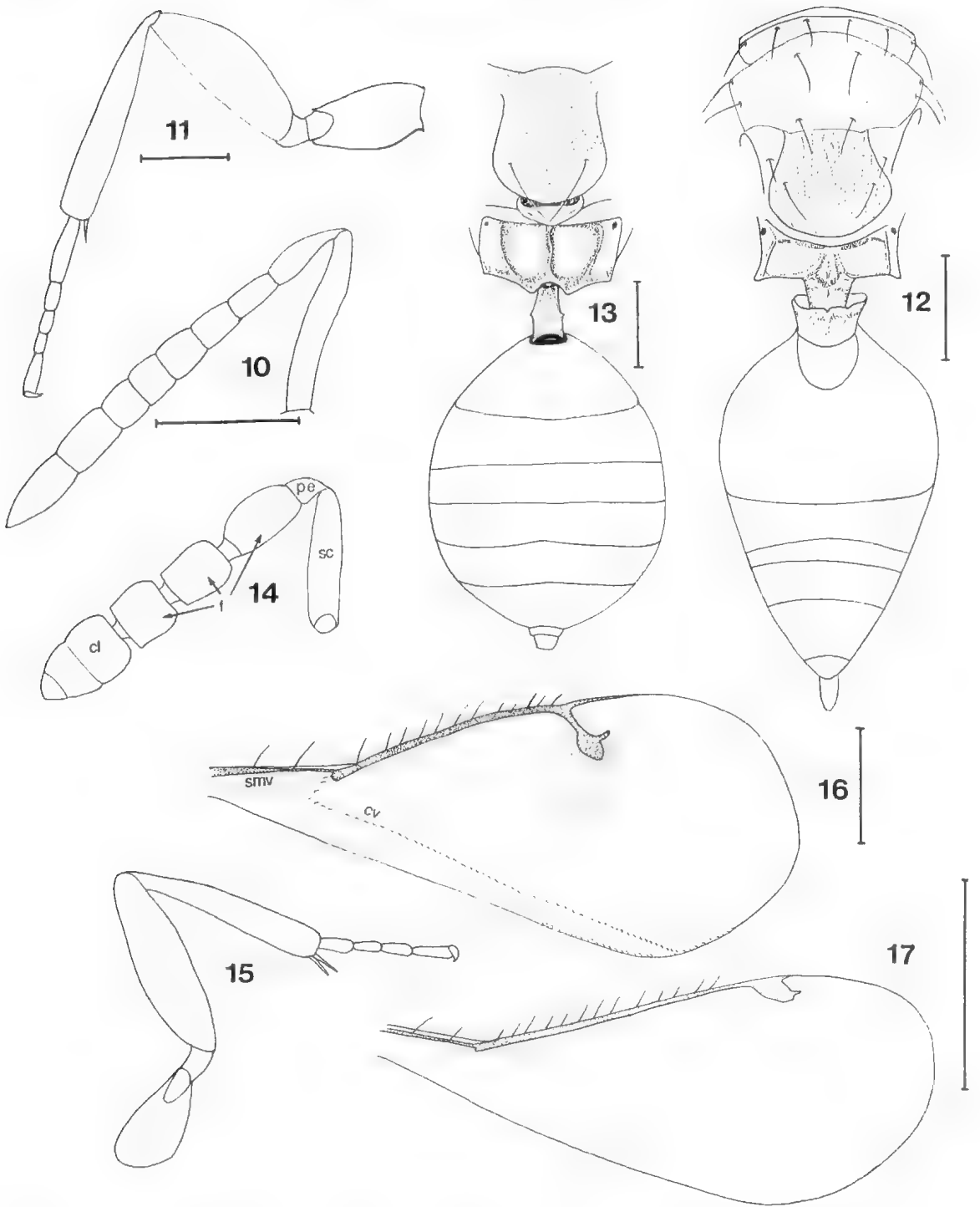
Usually only one *Cirrospilus* larva was found feeding on a host and generally it did not confine its feeding to one feeding site, as indicated by numerous dark melanised spots found over the host's integument. In the laboratory, *C. margiscutellum* held at room temperature took 16-17 days to complete development, once emerged from the egg. Mature *Cirrospilus* larvae

could be recognised from those of the other common parasitoids in the complex by the absence of long setae over the body and the presence of ampullae on both the dorsal and ventral surfaces. The larvae of different species of *Cirrospilus* could not be separated. Adults of *Cirrospilus* spp. can be distinguished from other eulophids in the complex by the presence of a submedial groove on the scutellum, submarginal vein with at least two bristles, and their metallic and/or striking colour patterns. *C. margiscutellum* is the only member of the genus in this complex to have the face with transverse black bands.

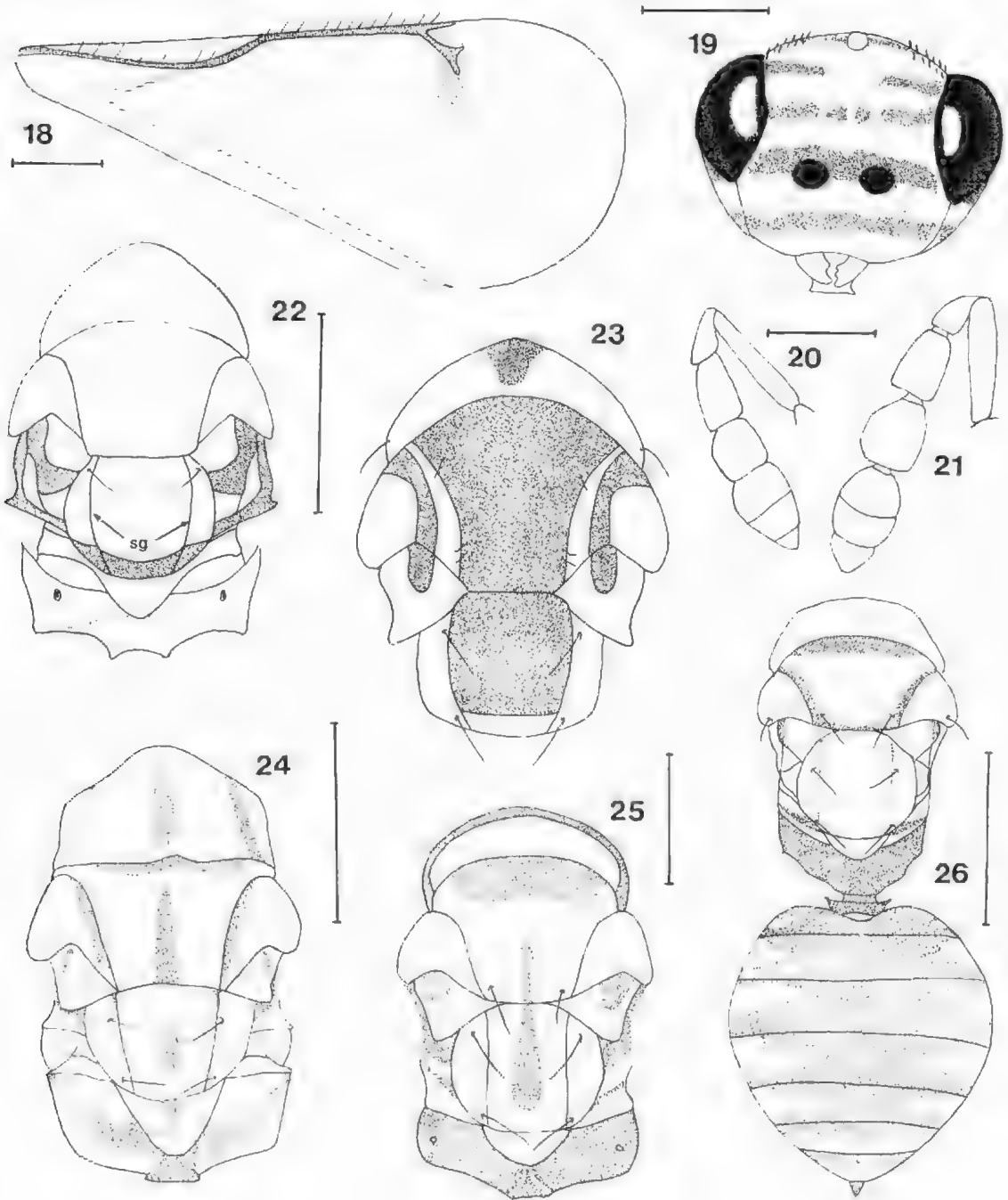
C. occipitis Girault & *Cirrospilus* sp. 3-5 FIGS 20, 21, 23-26

Four other species of *Cirrospilus* were reared from *P. froggatti* mines, all of which are solitary primary ectoparasitoids, with the exception of *Cirrospilus* sp. 3 which was found to be gregarious. *C. occipitis* and sp. 5 were observed to feed on host pupae, and sp. 3 and sp. 4 on the larval stages. *C. occipitis* and sp. 4 were found in mines over the summer months, early December to late March, and early January to late March, respectively, while sp. 3 and sp. 5 were recorded from only a few samples in one week in early March and late March, respectively. The five species encountered here can be separated relatively easily by their distinctive colour patterns.

Figs 5-9, 5-6, Fore and hind wings; 5, *Paraphylax* sp.; 6, *Bracon confusus* Austin. ♀; 7-9, Lateral view of whole body; 7, *Brachymeria* sp.; 8, *Eupelmus* sp.; 9, *Elasmus australiensis* Girault. Scales: Figs 5, 6 = 1.0 mm; Figs 7-9 = 0.5 mm. Abbreviations: bu = bullae; hc = hind coxa; hf = hind femur; mp = mesopleuron; pp = prepectus; pv = postmarginal vein; sv = stigmal vein.



Figs 10-17. 10-11, *Lariophagus* sp.: 10, antenna; 11, hind leg; 12, *Pediobius* sp., dorsal view of mesosoma and metasoma; 13, *Apleurotropis* sp., dorsal view of scutellum, propodeum and metasoma; 14-15, *Diaulomorpha* sp.: 14, antenna; 15, hind leg; 16-17, Fore wings: 16, *Chrysonotomyia* sp. 1; 17, *Chrysonotomyia* sp. 2. Scales: Figs 10, 14 = 0.5 mm; Figs 11, 15 = 0.5 mm; Fig. 12 = 0.5 mm; Fig. 13 = 250 μ m; Fig. 16 = 200 μ m; Fig. 17 = 0.5 mm. Abbreviations: cl = clava; cv = cubital vein; f = funicular segments; pe = pedicel; sc = scape; smv = submarginal vein.



Figs 18-26. 18-19, *Cirrospilus margiscutellum* (Girault): 18, fore wing; 19, anterior view of head showing transverse banding; 20-21, antennae: 20, *Cirrospilus occipitis* Girault; 21, *Cirrospilus* sp. 4; 22-25, *Cirrospilus* spp., dorsal view of mesosoma showing colour pattern: 22, *Cirrospilus margiscutellum* (Girault); 23, *Cirrospilus occipitis* Girault; 24, *Cirrospilus* sp. 3; 25, *Cirrospilus* sp. 4; 26, *Cirrospilus* sp. 5, dorsal view of mesosoma and metasoma showing colour pattern. Scales: Figs 18, 19 = 0.5 mm; Figs 20, 21 = 200 μ m; Figs 22, 23 = 0.5 mm; Figs 24, 25 = 250 μ m; Fig. 26 = 0.5 mm. Abbreviation: sg = submedial groove on scutellum.

Key to the parasitoids of *Phylacteophaga froggatti* in the Adelaide region (based on females)

- 1 Fore wing with more than one enclosed cell (Figs 5, 6); prepectus absent 2
- 2 Fore wing with no more than one enclosed cell (Figs 7, 16-18); prepectus usually present (Figs 8, 9), sometimes absent (Fig. 7) (Chalcidoidea) 4
- 3 Fore wing with vein 2m-cu present; hind wing with vein r-m meeting Rs after Rs diverging from Sc + R (Fig. 5) (Ichneumonidae) [fore wing with two bullae in 2m-cu (Fig. 5), mesoscutum smooth and unsculptured] *Paraphylax* sp.
- 4 Fore wing with vein 2m-cu absent; hind wing with vein r-m meeting Rs before Rs diverging from Sc + R (Fig. 6) (Braconidae) 3
- 5 Vertex, occiput and temples mostly hairless except for row of short hairs around margin of eyes and posterior vertex (Fig. 3); propodeum black *Bracon phylacteophagus* Austin
- 6 Vertex, occiput and temples sparsely covered with long hairs (Fig. 4); propodeum orange-yellow *Bracon confusus* Austin
- 7 Hind femur enlarged and with teeth on ventral edge (Fig. 7); prepectus very small, virtually absent (Chalcidoidea) [malar suture distinct; postmarginal vein longer than stigmal vein (Fig. 7); propodeum with rough alveolate sculpturing] *Brachymeria* sp.
- 8 Hind femur not enlarged and without teeth (Figs 8, 11); prepectus distinct (Figs 8, 9) 5
- 9 Mesopleuron greatly enlarged, convex, developed into a large undivided shield (Fig. 8) [postmarginal vein slightly shorter than stigmal vein; ovipositor protruding from posterior mesosoma, sheaths black with middle third white (Fig. 8)] *Eupelmus* sp.
- 10 Mesopleuron not greatly enlarged (Fig. 9) 6
- 11 Hind coxa developed as a large flat disc (Fig. 9); hind tibia with setae forming distinct criss-cross pattern; fore wing narrow, postmarginal vein much longer than stigmal vein (Fig. 9) (Elasmidae) [body dark, tegula and legs pale except for hind coxae] *Elasmus australiensis* Girault
- 12 Hind coxa not as a large flat disc (Fig. 11); hind tibia hairs not forming criss-cross pattern; fore wing relatively broad (Figs 16-18) 7
- 13 Hind tarsi 5-segmented (Fig. 11); antenna without distinct funicular segments and clava (Fig. 10) (Pteromalidae) [head round in anterior view; basal third of fore wing virtually devoid of hairs] *Lariophagus* sp.
- 14 Hind tarsi 4-segmented (Fig. 15); antenna with distinct funicular segments and clava (Figs 14, 20, 21) (Eulophidae) 8
- 15 Dorsal mesosoma with long stout hairs (Fig. 12); metasoma distinctly petiolate (Figs 12, 13), body black and shiny 9
- 16 If dorsal mesosoma with hairs then mostly fine and short; metasoma sessile, or petiole less conspicuous (Fig. 26); body colour variable 10
- 17 Scutellum longitudinally strigose with exception of longitudinal medial line which is smooth (Fig. 12); T1 of metasoma with anterior flange (Fig. 12); legs all black except proximal 3 tarsal segments of mid and hind legs which are white *Pediobius* sp.
- 18 Scutellum with coriaceous sculpturing (Fig. 13); T1 of metasoma without flange (Fig. 13); all legs distal to coxae pale in colour *Apleurotopis* sp.
- 19 Funicle of antennae 3-segmented (Fig. 14) [body metallic green-gold in colour, all legs distal to coxae white; body about 2 mm in length] *Dialtomorpha* sp.
- 20 Funicle of antennae 2-segmented (Figs 20, 21) 11
- 21 Scutellum without submedial grooves; submarginal vein with 2 dorsal bristles (Figs 16, 17); body less than 1 mm in length (*Chrysonotomyia* Ashmead) 12
- 22 Scutellum with submedial grooves (Figs 22, 23); submarginal vein with more than 2 dorsal bristles (Fig. 18); body greater than 1 mm in length (*Cirrospilus* Westwood) 13
- 23 Cubital vein of fore wing indicated by a single row of hairs (Fig. 16); stigmal vein distinct and infusate around distal end (Fig. 16); mesosoma and head metallic green *Chrysonotomyia* sp. 2
- 24 Cubital vein of wing not indicated (Fig. 17); stigmal vein short and not infusate (Fig. 17); mesosoma and head non-metallic and dark in colour *Chrysonotomyia* sp. 1
- 25 Clava of antenna continuous with funicular segments (Fig. 20) 14
- 26 Clava separated from funicular segments by distinct constriction between segments (Fig. 21) 16
- 27 Stigmal vein infusate around distal end, sometimes only faintly (Fig. 18); vertex with short stout black hairs (Fig. 19) 15
- 28 Stigmal vein without infuscation distally; vertex with only fine pale hairs [mesosoma with yellow and metallic green markings (Fig. 23)] *Cirrospilus occipitis* Girault
- 29 Dorsal mesosoma metallic green-blue with slight yellow markings in posterior half (Fig. 22), surface with reticulate sculpturing; face with transverse dark stripes (Fig. 19); pronotum shorter than scutum (Fig. 22) *Cirrospilus margiscutellum* (Girault)
- 30 Pronotum yellow with 3 longitudinal black bands; rest of mesosoma orange with black markings (Fig. 24); surface with coriaceous sculpturing; pronotum nearly as long as scutum *Cirrospilus* sp. 3
- 31 Metasoma rounded in dorsal view; pronotum yellow-orange, rest of dorsal mesosoma orange with black markings (Fig. 26) *Cirrospilus* sp. 5
- 32 Metasoma broadly elongate, pointed posteriorly; dorsal mesosoma yellow with black markings (Fig. 25) *Cirrospilus* sp. 4

Discussion

This study confirms a number of aspects of the biology of *P. froggatti* first reported by Farrell & New (1980), as well as documenting the fecundity and longevity of adults, and details of its parasitoid complex for the first time. Previously, this insect had been recorded only as a sporadic pest of eucalypts in the Adelaide region and then mostly on ornamental trees. However, the status of *P. froggatti* as an emerging serious pest both in Australia and New Zealand has increased dramatically over the last few years and this is correlated with a corresponding expansion in native woodland plantings in south-eastern Australia. Indeed, the Engineering & Water Supply Department of South Australia has rated *P. froggatti* as one of the most important pests at its Bolivar woodland (pers. comm. S. Shaw).

During this study we recorded nearly three times the number of parasitoid species associated with *P. froggatti* as any reported by previous authors (Riek 1955; Farrell & New 1980; Curry 1981). The size of the parasitoid complex in the Adelaide region, however, is unlikely to be significantly larger than elsewhere in

Australia. Rather, the concentration of this study on rearing parasitoids and its longer duration has meant that several rarer species have been collected. Also, the taxonomy of the groups involved is now better known (see in particular Bouček 1988 and Austin & Faulds 1989), so that species can be more easily and reliably identified. However, the makeup of the parasitoid complex and relative abundance of species does seem to differ between regions. For instance, in the Adelaide region *Cirrospilus* sp. 1 was far more abundant than *B. phylacteophagus*, while in Melbourne the latter species was more abundant (Farrell & New 1980). In Western Australia Curry (1981) reared six parasitoids from *Phylacteophaga* (three *Cirrospilus* spp., *Elasmus* sp., *Eupelmus* sp., an unnamed eulophid and *Apanteles* sp.) but no *Bracon*. Austin & Faulds (1989) have pointed out that the record of *Apanteles* sp. must be erroneous as members of this genus and all microgasterine braconids are endoparasitoids of lepidopteran larvae. The only major parasitoid taxon not recorded in this study is *Isopluoides westralionus* Girault, a pieromalid, which has been reared from *P. froggatti* only in Western Australia (Bouček 1988).

Farrell & New (1980) suspected the *Cirrospilus* sp. reared by them in Melbourne to be polyphagous and to use alternative hosts at different times of the year to breed continuously. Although we did not rear

parasitoids from other eucalypt leaf minings in the Adelaide region, the fact the multiple *Cirrospilus* species have often been recorded from other hosts does provide some indirect evidence that members of this parasitoid genus are polyphagous (pers. comm. N. Gough, I. D. Naumann).

This study should provide a solid basis for more detailed work on the ecology of *P. froggatti*, particularly the factors that influence its abundance, means of overwintering, and the susceptibility of its eucalypt species. These and other factors will be important in understanding how *P. froggatti* develops as a pest and how best it can be controlled. Programs aimed at limiting the damage caused by this sawfly will need to take into account the mortality caused by the above parasitoids. In this respect future research might profitably examine both seasonal and regional differences in rates of parasitism and the species involved.

Acknowledgments

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SOUTH AUSTRALIA, WITH A KEY TO SPECIES OF
THE ELMINIINAE**

*By D. E. BAYLISS**

Summary

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Three new species of intertidal barnacles from South Australia are described. *Elminius flindersi* sp. nov. is a comparatively large species, grey to white in colour which favours habitats with strong water movement although not direct wave action. It has a long hatchet shaped tergum with a centrally localised fold. In comparison with congeners the shell is strong and the cirri are broad and robust. *E. placidus* sp. nov. is a smaller and more fragile species found in very sheltered localities, including mangroves in the Spencer Gulf. It can be distinguished by its banded shell and wedge-shaped tergum. The body and cirri are very elongated. *E. erubescens* sp. nov. is common in the high intertidal zone in the Adelaide region. It is easily distinguished by the reddish coloration of its translucent shell which gives a dark purple appearance on rock.

It is suggested that South Australia has Elminiinae distinct from those of the Eastern States of Australia.

Key Words: Cirripedia, *Elminius flindersi* sp. nov., *Elminius placidus* sp. nov., *Elminius erubescens* sp. nov., *Elminius modestus*, *Elminius adalaidae*, *Elminius covertus*, intertidal, South Australia, taxonomy.

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Introduction

In South Australia barnacles belonging to the genus *Elminius* are highly abundant (Womersley & Edmonds 1958; Hutchings & Recher 1982; Bayliss 1982). Until recently, they were classified as *Elminius modestus* Darwin, as were those found in eastern Australia, Western Australia and New Zealand. This situation arose from the very broad definition of this species obtained from a combined examination of Darwin's (1854) original description and illustrations with those of Pope's (1945) paper.

Foster (1980) suggested that Pope's description confused a new species with *E. modestus* as known in New Zealand (Moore 1944; Morton & Miller 1968; Foster 1978) and that Darwin's original material may also have been a combination of these two species. The new species, *E. covertus*, was subsequently described by Foster (1982) together with a six-plated barnacle, *Hexaminus popeiana*, A new subfamily, Elminiinae, was proposed to accommodate them. Studies of larvae by Egan & Anderson (1985) support the establishment of this subfamily.

Foster (1982) furthermore suggested that *E. modestus* was a New Zealand species which had been introduced into Australia by fouling on shipping, probably in the nineteenth century; *E. covertus* was, therefore, the only known endemic Australian species. Bayliss (1988) described another species, *E. adalaidae*, which is abundant in the Adelaide region, and suggested that

E. covertus was not found in South Australia although *E. modestus* was present. Jones (1990) has identified both *E. covertus* and *E. modestus* from southern Western Australia.

There is little fossil material, but Buckeridge (1982) has described *E. chapronierei* from the lower Miocene in Victoria and *E. pomahakensis* from the upper Oligocene in New Zealand (Buckeridge 1984) and suggested the subfamily originated in south-east Australia. He proposed a two-phased migration from Australia to New Zealand and South America, firstly in the Oligocene for *Elminius* with a spur on the tergum and subsequently, in the Cenozoic, for *Elminius* lacking a spur.

This paper describes three new species of *Elminius* which, with *E. modestus* and *E. adalaidae*, brings to five the number of species of this genus found in South Australia.

Systematics

Suborder Balanomorphia Pilsbry, 1916
Superfamily Balanoidea Leach, 1817
Family Archaeobalanidae Newman and Ross, 1976
Subfamily Elminiinae Foster, 1982
Genus *Elminius* Leach, 1825

Type species *Elminius kingii* Gray, 1831

Elminius flindersi sp. nov.
FIGS 1, 3

Holotype: SAM C4242, on iron pilings of ferry jetty, Penneshaw, Kangaroo Island, South Australia; 35°44'S, 137°57'E; D. Bayliss, 21.vii.1992; dissected (partially).

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Current address: 7 Thomas Street, Kingsgrove, N.S.W. 2208

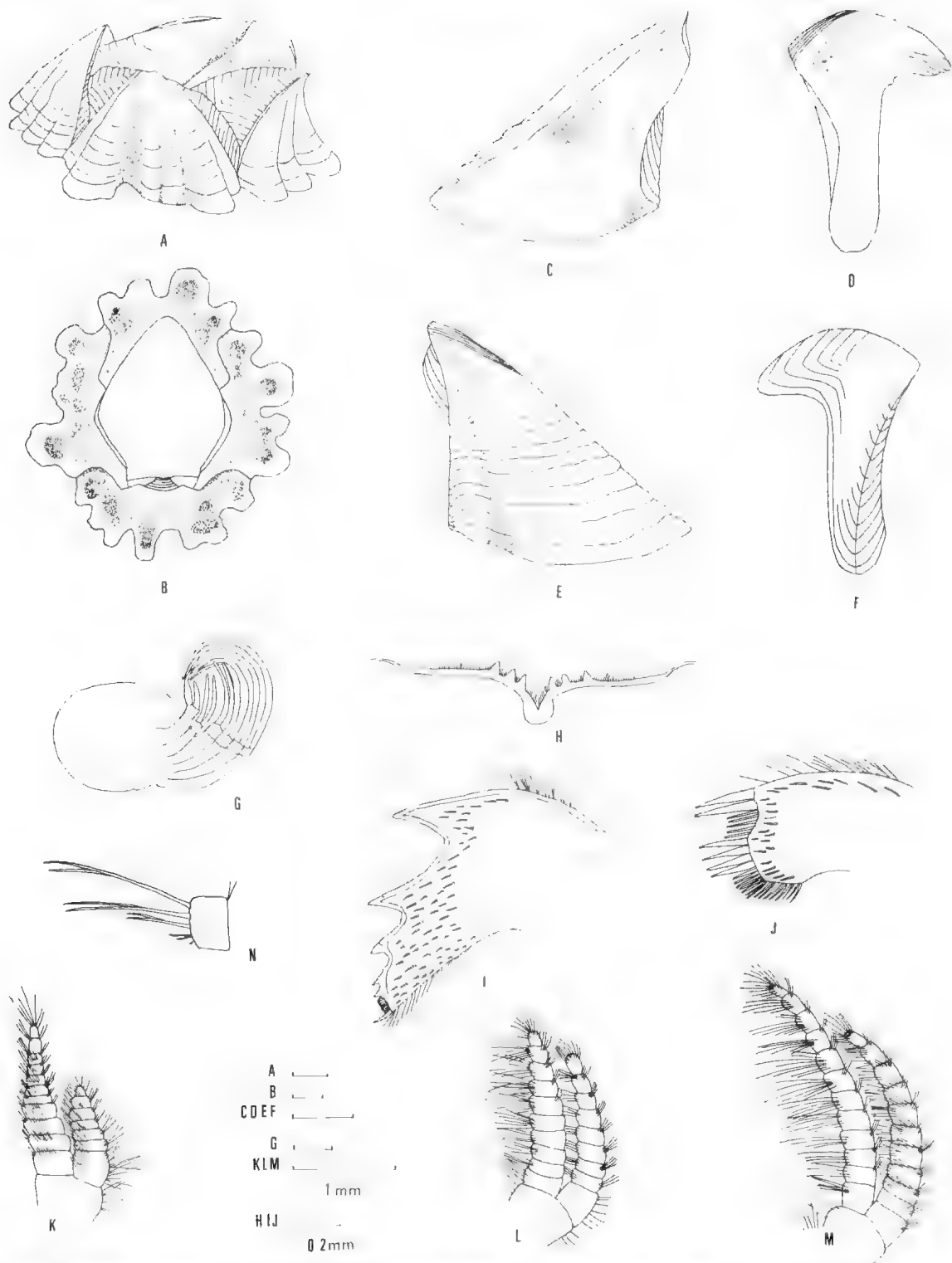


Fig. 1. *Elminius flindersi* sp. nov. holotype. A. External view of shell; B. inner view of shell; C. scutum, internal view; D. tergum, internal view; E. scutum, external view; F. tergum, external view; G. body; H. labrum; I. mandible; J. maxillule; K-M. cirri I-III; N. middle segment, posterior ramus, cirrus VI.

Paratypes: SAM C4243, WAM 727-92; D. Bayliss, 21.vii.1992, same locality as holotype.

Description of holotype: Shell (Figs 1A, 1B): conical, white to grey, opaque. Parieties folded. Orifice pentagonal in outline, width $\frac{1}{4}$ length, carinal sides almost twice as long as lateral sides, rostral side straight. Basal outline sinuous, deeply undulating. Alae wider than radii with less oblique summits. Radii with oblique summits, narrow. Shell 10mm in basal diameter, 9.5mm in width, 4mm in height.

Opercula (Figs 1C, 1D, 1E, 1F): Solid white to grey in colour. Scutum longer than high, basal margin slightly convex with slight upward turning at tergal corner, crests for depressor muscles absent, articular ridge, articular furrow moderately developed, adductor ridge not apparent, adductor pit faint, externally growth ridges present.

Tergum hatchet shaped, vertical articular ridge folding inward to form centrally limited fold, articular margin gently curving in apical region from carinal margin, becoming parallel with basal margin to form long narrow handle, basal margin curving sharply, almost at right angles, to form projection with carinal margin, projection with prominent, deeply curved crests for tergal depressor muscles, spur confluent with basiscutal angle.

Body (Fig. 1G): prosoma white, broad, rounded. Cirri light reddish brown in living specimens, cirri I, II and III slightly darker than cirri IV, V and VI, colour lost on preservation.

Mouthparts (Figs 1H-1J): Labrum with three teeth and setulae, on each side of central notch. Mandible with five teeth, lower short pectinate edge terminating in short curved spine. Maxillule with two large spines above notch, five smaller spines in notch, four large spines below notch, smaller spines at lower angle.

Cirri (Figs 1K-1N): Cirrus I with anterior ramus $\times 1.5$ length of posterior ramus, segments broad, slightly protuberant. Anterior ramus of cirrus II slightly longer than posterior ramus, segments slightly protuberant anteriorly. Cirrus III with anterior ramus slightly longer than posterior ramus, segments slightly protuberant anteriorly; setae on both rami extremely long, stout pectinate setae on six distal segments of posterior ramus. Cirri IV to VI all subequal in length, segments with three large pairs, two small pairs of setae on anterior face, small proximal pair of setae between segments. Number of segments in rami of cirri I-VI shown in Table 1.

Penis: Penis as long as cirrus VI, setose, basidorsal point absent.

Variation: Shell can be tubular, conical or flattened. Parieties can be smooth or undulating with variable number of longitudinal folds. Maximum basal diameter 17mm. Colour varies from white to light grey.

Etymology: The species name refers to the Flindersian biogeographic region.

Comparison with other species: *Elminius flindersi* is larger and more robust than other members of the genus found in Australia. The shell is thicker and comparatively strong. The opercular plates are opaque rather than translucent. The body is broad and rounded with broad cirri.

E. flindersi cannot be reliably distinguished from *E. modestus* on the basis of external shell appearance. The opercular plates are, however, quite different. The tergum (Fig. 1D, 1F) is hatchet shaped with a long handle and an articular furrow which is restricted to the central portion.

E. modestus (Fig. 2B, 2D) has a deep articular fold running from the apical end to almost the basiscutal angle. The articular margin, unless worn, is straight. The scutum (Fig. 2C) has a grey band, but this feature is not always apparent.

TABLE 1. Cirral counts. *Elminius flindersi* sp. nov. (anterior ramus first).

Basal diameter (mm)	Cirrus					
	I	II	III	IV	V	VI
10.0 (holotype)	11,7	10,9	12,11	22,20	24,25	26,27
5.0	12,6	10,1	12,11	18,17	21,20	23,22
8.0	12,7	11,11	13,13	21,20	23,24	26,25
8.0	12,7	10,9	13,13	23,23	27,27	27,28
10.0	11,7	11,10	13,11	22,19	24,23	23,23



Fig. 2. *Elminius modestus* Darwin. A, scutum, internal view; B, tergum, internal view; C, scutum, external view; D, tergum, external view.

E. modestus also can be distinguished from other members of the genus in lacking pectinate setae on the posterior ramus of cirrus III. The opercular flaps are pure white with a grey band at the rostral end and a small orange dot centrally. *E. flindersi* has a dark brown band at the rostral end and another brown band centrally on flaps which are dull white.

E. adelaidae (Bayliss 1988 Fig. 2B) has a very small articular furrow, which may not be visible if the tergum is viewed directly from above. The shell is much thinner, translucent, and is light brown. The opercular flaps are, however, no close to *E. flindersi* in appearance to be useful for identification.

Habitat: *Elminius flindersi* is found in the intertidal zone in waters sheltered from direct wave action. It is found in habitats with stronger water flow and more turbulence than other members of the genus in South Australia. In the gulf regions, where wave impact is diminished, it occurs on exposed rocks. It grows in

large sizes on jetties although it is not found on surfaces facing directly into waves at more exposed localities. Outside the gulf regions it is found in habitats protected from oceanic waves such as in boat enclosures behind breakwaters.

Settlement occurs on a wide variety of surfaces including rocks, cement, wood, metal and plastic. It is rarely found in mangroves where water flow is gentle. At Port Pirie it can be found on rocks in the strongly-flowing sections of the tidal river, but not in nearby mangroves.

Distribution: *Elminius flindersi* is widespread in South Australia from Kangaroo Island to Ceduna and the western Eyre Peninsula, and occurs in both gulfs (Fig. 3). In the Spencer Gulf it can be found at Port Augusta indicating that it can tolerate the wide salinity and temperature range found in South Australian waters.

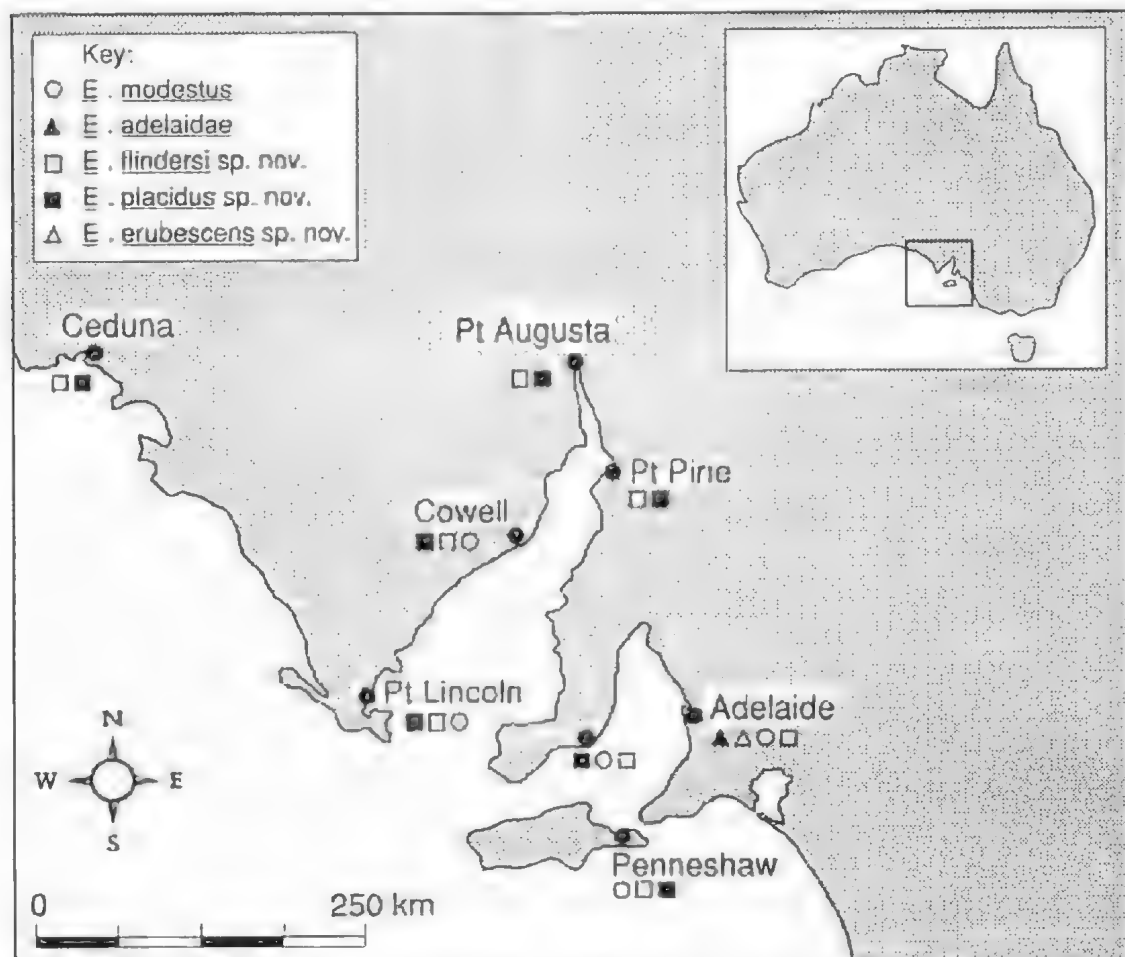


Fig. 3. Distribution of *Elminius modestus* Darwin, *Elminius adelaidae* Bayliss, *Elminius flindersi* sp. nov., *Elminius placidus* sp. nov. and *Elminius erubescens* sp. nov. in South Australia.

Elminius placidus sp. nov.
FIGS 3, 4

Elminius modestus: Womersley & Edmonds 1958: 243, Thomas & Edmonds 1979: 161, Hutchings & Recher 1982: 95.

Holotype: SAM C4244, on branches of *Avicennia marina* at Cowell, South Australia, 33°68'S, 136°94'E; D. Bayliss, 6.ii.1992; dissected (partially).

Paratypes: SAM C4245, WAM 728-92, D. Bayliss, 6.ii.1992. Same locality as holotype.

Description of holotype: Shell (Fig. 4A, 4B): upright conical, grey to white with thin brown and dark grey bands parallel to base. Parieties gently folded. Shell thin and nearly translucent. Orifice large, pentagonal in outline, rostral side concave and broad, carinal sides longer than lateral sides, width $\frac{1}{4}$ length. Basal outline sinuous. Alae wider than radii with less oblique summits. Radii with oblique summits, narrow radii and alae with prominent growth lines. Shell 7 mm in basal diameter, 5 mm in width, 5 mm in height.

Opercula (Figs 4B-E): thin, translucent, white in colour, grey margin near articulating margins of internal surfaces of tergum and scutum. Scutum longer than high, basal margin slightly convex with prominent depression for depressor muscles, no crests apparent, articular ridge, articular furrow moderately developed, adductor ridge, adductor pit not apparent, externally growth ridges present.

Tergum wedge shaped, articular margin and basal margin gently curving from apical end, converging on basiscutal angle, articular furrow shallow, apical portion large with small, feeble crests for tergal depressor muscles; spur confluent with basiscutal angle.

Body (Fig. 4G): Prosoma white, narrow, elongated, palps and cirri I to III very dark brown, cirri IV to VI light brown with dark brown pigment along anterior face of segments, cirrus I covering oral cone.

Mouthparts (Figs 4H-J): Labrum with three teeth and setulae on each side of central notch. Mandible with five teeth, lower pectinate edge terminating in short curved spine. Maxillule with two large spines above notch, five smaller spines in notch, four large spines below notch, smaller spines at lower angle.

Cirri (Figs 4K-N): Cirrus I with anterior ramus $\times 1.7$ length of posterior ramus, anterior ramus with broad proximal segments, narrow distal segments, with long setae, segments slightly protuberant. Anterior ramus of cirrus II slightly longer than posterior ramus, segments slightly protuberant anteriorly. Cirrus III with anterior ramus $\times 1.25$ length of posterior ramus, segments slightly protuberant anteriorly, setae on ramus very long, stout pectinate setae on six distal segments of posterior ramus. Cirri IV to VI all subequal in length, segment with four large pairs, two small pairs of setae on anterior face, small proximal pair of setae between segments, anterior face with dark brown

pigment. Number of segments in ratio of cirri I to VI shown in Table 2.

TABLE 2. Cirral counts: *Elminius placidus* sp. nov. (anterior ramus first).

Basal diameter (mm)	Cirrus					
	I	II	III	IV	V	VI
7.0 (holotype)	14,8	10,10	13,13	27,24	28,30	32,30
4.0	14,6	9,9	12,12	24,21	26,25	31,29
4.0	12,6	10,10	11,11	24,23	26,24	30,26
5.0	14,7	10,9	14,13	23,23	27,27	29,27
6.0	14,8	10,10	14,13	25,24	28,23	28,27

Penis: Penis as long as cirrus VI, setose, basidorsal point absent.

Variation: Shell is usually upright conical or tubular and rarely flattened. Shell may have visible banding, but $\times 10$ magnification is often required to see the dark and light bands. On mangroves the barnacles may appear solidly grey. Some specimens collected from rocks have dark grey bands and the shell may appear almost bluish. Thomas & Edmonds (1979) described the shell as being 'bluish-green'. Some specimens have a slight pink tinge towards the top of the parietes.

The tergum is extremely thin near the basal margin and wear may alter the shape. In some specimens the tergum is virtually triangular with the basal margin very gently curving from the tergal crests to the basiscutal angle. On unworn specimens, the external surface of the tergum is grey with a white area at the apical end.

The scutum in many specimens has a nearly straight basal margin and the articular margin is almost at right angles forming a right angle triangle shape. The depression for the depressor muscle is usually well formed with the shell being extremely thin in this area.

Etymology: The species name is derived from the Latin *placidus* meaning calm, tranquil with reference to the habitat of this species.

Comparison with other species: The shell is thin and translucent with narrow dark bands. Other species are uniform in colour and lack the alternating light and dark banding. The opercular plates are thin with grey margins internally along the articulating margins.

The tergum is distinctive in shape. The apical region is large with very feeble crests. The articular margin and the basal margin curve gently to the basiscutal angle forming a triangular or wedge shape.

The prosoma is narrow and elongated as are the cirri. The dark colour of the cirri contrasts with the white prosoma. The coloration survives preservation.

The opercular flaps are cream with a dark black band at the rostral end and another black band centrally. This enables it to be distinguished from *E. modestus*, but it cannot be readily distinguished from other South Australian species which have the same pattern of dark bands on lighter coloured flaps.

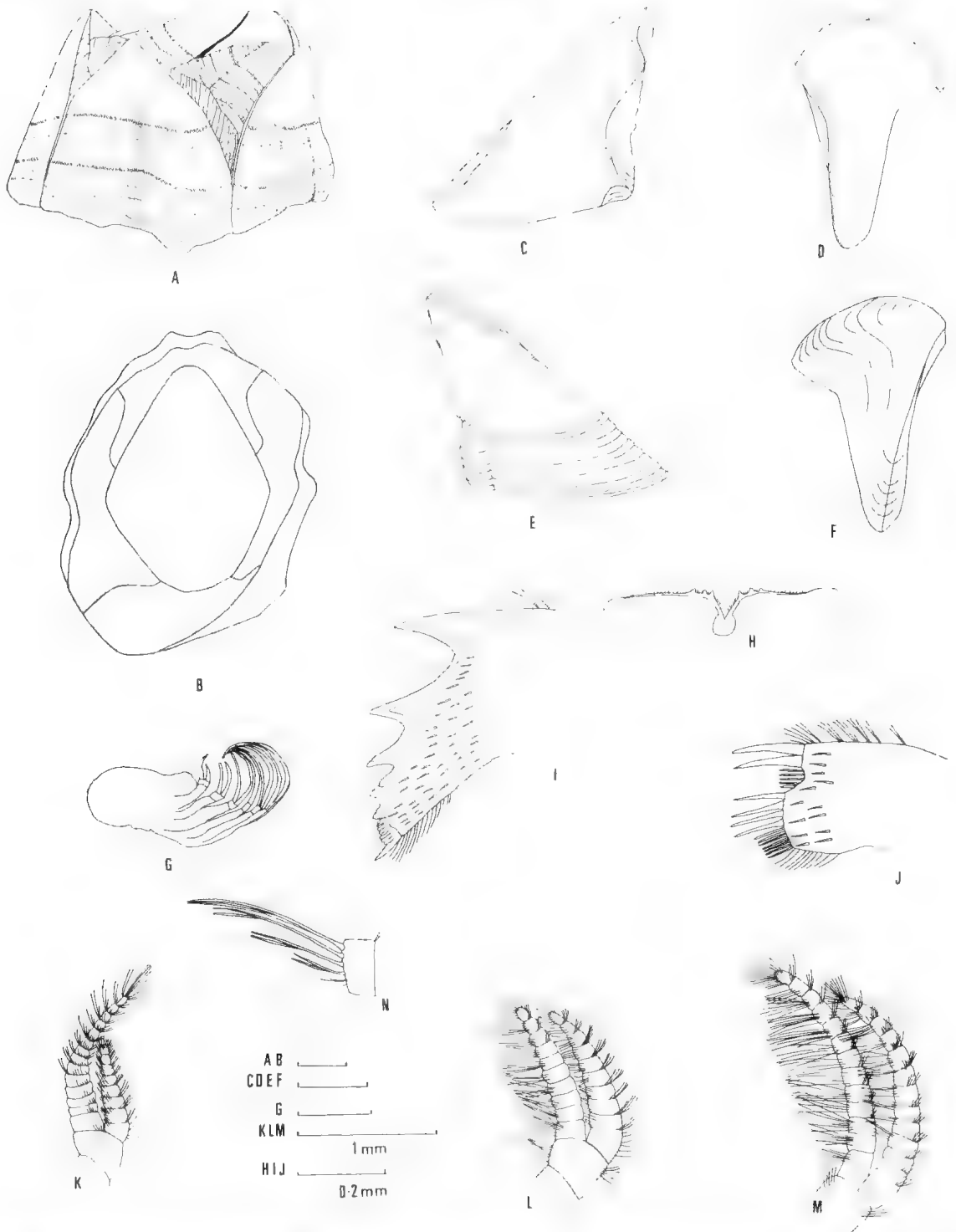


Fig. 4. *Elminius placidus* sp. nov. holotype. A. External view of shell; B. inner view of shell; C. scutum, internal view; D. tergum, internal view; E. scutum, external view; F. tergum, external view; G. body; H. labrum; I. mandible; J. maxillule; K-M. cirri I-III; N. middle segment, posterior ramus, cirrus VI.

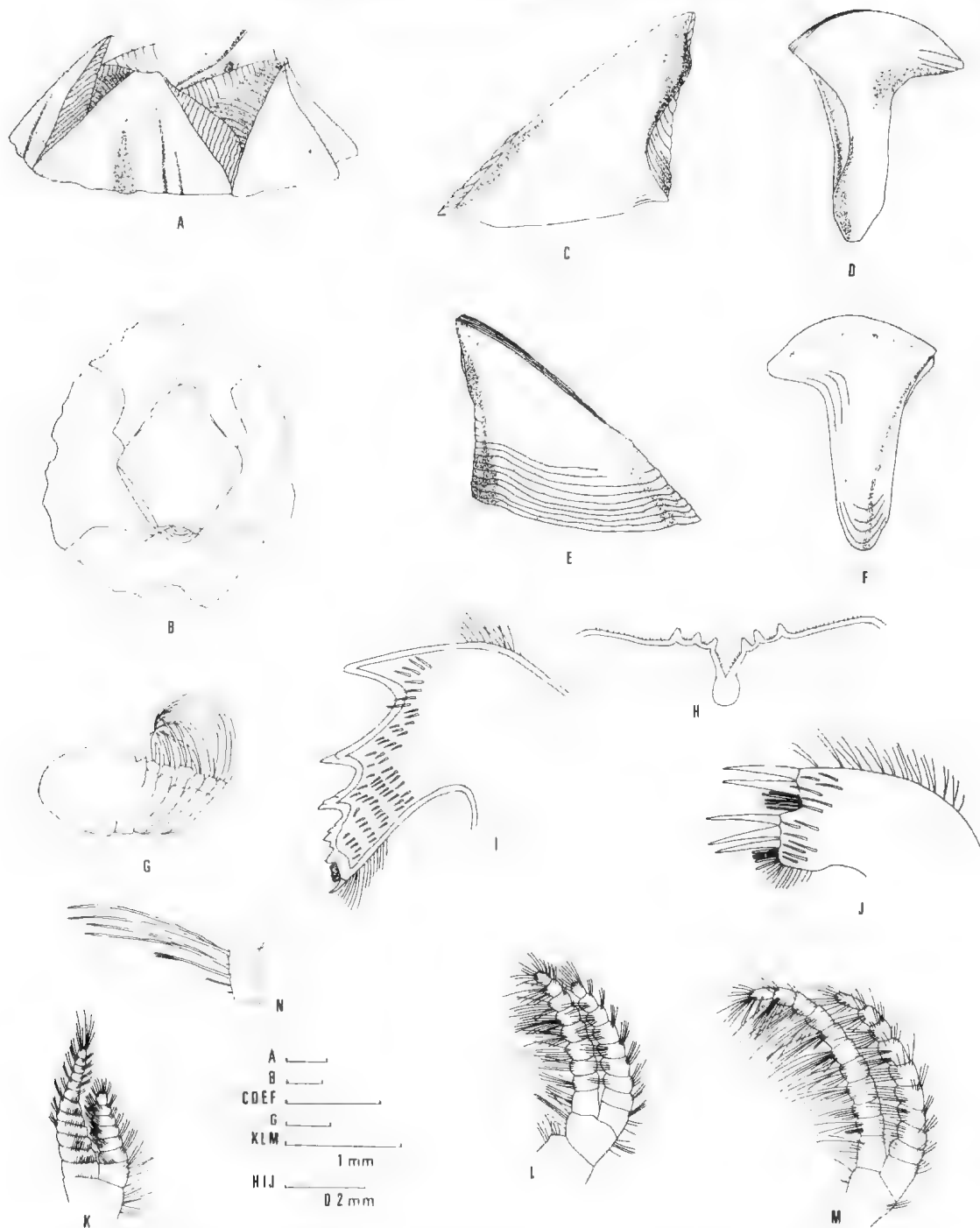


Fig. 5. *Elminius erubescens* sp. nov. holotype. A. External view of shell; B. inner view of shell; C. scutum, internal view; D. tergum, internal view; E. scutum, external view; F. tergum, external view; G. body; H. labrum; I. mandible; J. maxillule; K-M, cirri I-III; N. middle segment, posterior ramus, cirrus VI.

Habitat: *Elminius placidus* is an intertidal species which is found in sheltered habitats. It is highly abundant in mangroves in Spencer Gulf. It settles on branches and pneumatophores, but is rarely found on leaves. It is not restricted to mangroves but also settles on rocks, cement, wood, metal and other surfaces.

Distribution: *Elminius placidus* is widespread, being found on Kangaroo Island, Yorke Peninsula, Spencer Gulf and Eyre Peninsula (Fig. 3). It is not found in the mangroves north of Adelaide which are occupied by *E. adalaidae*.

***Elminius erubescens* sp. nov.**
FIGS 3, 5

Elminius covertus Foster 1982: 26.

Holotype: SAM C4246, collected on rubber tyres at Glenelg boat ramp, Adelaide, South Australia, 34°56'S, 138°36'E, D. Bayliss, 19.vi.1991, dissected (partially).

Paratypes: SAM C4247, WAM 729-92, D. Bayliss, 19.vi.1991, from the same locality as holotype.

Description of the holotype: Shell (Figs 5A, 5B): flattened conical, translucent with red coloration, appearing dark purple before the body removed, colour greyish purple when preserved. Parieties gently folded. Orifice small, pentagonal in outline, width $\frac{1}{4}$ length, rostral side short and straight, other sides almost equal in length. Basal outline sinuous. Alae wider than radii, with less oblique summits. Radii with oblique summits, narrow. Shell 8mm in basal diameter, 7mm in width, 3mm in height.

Opercula (Figs 5C-F): Thin translucent, reddish, greyish purple with white areas when preserved. Scutum longer than high, basal margin slightly convex with upward turning at tergal corner, articular ridge, articular furrow moderately developed, apex reflected outwards, externally growth ridges apparent.

Tergum with articular ridge folding inwards to form well developed furrow, articular margin concave, basal margin curving sharply to form projection with carinal margin, well developed crests for tergal depressor muscles, spur confluent with basiscutal angle.

Body (Fig. 5G): Prosoma light brown, palps and cirri I and II with some dark brown pigment, cirri III to VI clear, partially light brown, preserved material with body and cirri almost uniformly light brown, prosoma and cirri elongated, cirrus I overlapping oral cone.

Mouthparts (Figs 5H-J): Labrum with three teeth and setulae on each side of central notch. Mandible with five teeth, lower short pectinate edge terminating in short curved spine. Maxillule with two large spines below notch, smaller spines at lower angle.

Cirri (Figs 5K-N): Cirrus I with anterior ramus $\times 1.5$ length of posterior ramus, segments slightly protuberant. Anterior ramus of cirrus II slightly longer

than posterior ramus, segments slightly protuberant anteriorly. Cirrus III with anterior ramus slightly longer than posterior ramus, segments slightly protuberant anteriorly; setae on both rami long, stout pectinate setae on six distal segments of posterior ramus. Cirrus IV to VI subequal in length, segments with three large pairs, two small pairs of setae on anterior face, small proximal pair of setae between segments. Number of segments in rami of cirri I to VI shown in Table 3.

TABLE 3. Cirral counts: *Elminius erubescens* sp. nov. (anterior ramus first).

Basal diameter (mm)	Cirrus					
	I	II	III	IV	V	VI
3.0 (holotype)	12,7	9,9	11,10	21,24	25,24	28,30
7.0	14,6	9,9	12,12	25,28	29,27	32,31
7.0	15,6	10,8	11,11	23,20	25,24	25,24
7.5	13,6	11,10	12,11	20,19	23,23	25,25
9.0	12,6	9,9	13,12	23,23	25,26	30,27

Penis: Penis as long as cirrus VI, setose, basidorsal point absent.

Variation: *Elminius erubescens* is usually flattened although tubular and upright conical forms can occur. The shell often has broad longitudinal folds which vary in number between specimens. Maximum basal diameter 12mm.

Etymology: The specific name is derived from the Latin *erubescere*, to blush with modesty, in reference to its redness.

Comparison with other species: *Elminius erubescens* can be easily distinguished from other species in South Australia by the red coloration of the translucent shell which, in the field, appears dark purple. The shell is otherwise close to *E. modestus*. It lacks the ridges seen in *E. covertus*, although worn specimens of the two species are similar in appearance. The tergo-seutal flaps are straw to pale yellow with two dark brown to black bands. A small portion of the flaps between the rostral end and the first dark band are white. *E. covertus* has six pairs of dark spots on white tergo-seutal flaps.

Habitat: *Elminius erubescens* is common in sheltered waters in the Adelaide region although it is not found in mangroves. It settles on a wide variety of surfaces including rock, cement, wood, metal and rubber. It is the highest barnacle in the intertidal zone. There is little overlap with *E. modestus* which forms a zone below it. On rocks it is usually found on surfaces which are overlapping or do not face directly into the afternoon sun, although it can stand exposure to sunlight for part of the day. *E. adalaidae* avoids sunlight and is found under rocks which are lower in the intertidal zone.

Distribution: This species is very common in the Adelaide region, but was not found elsewhere in South Australia (Fig. 3). Its distribution outside of South Australia is unknown.

Key to species of the Elminiinae

- | | | |
|---|---|--|
| 1 | Shell with four compartmental plates . . . | 2 |
| | Shell with six compartmental plates | 6 |
| 2 | Tergum with spur confluent with basiscutal angle | 3 |
| | Tergum with distinct spur | <i>Elminius kingii</i> Gray (South America) |
| 3 | Shell white or grey | 4 |
| | Shell not white or grey | 5 |
| 4 | Shell white, tergum with straight articular margin, deep articular furrow | <i>Elminius modestus</i> Darwin (Australia, New Zealand, Europe, South Africa) |
| | Shell greyish-white, tergum hatchet shaped, concave articular margin, centrally localised furrow | <i>Elminius flindersi</i> sp. nov. (South Australia) |
| | Shell grey, narrow dark bands alternating with white, tergum wedge shaped, weak crests, shallow furrow | <i>Elminius placidus</i> sp. nov. (South Australia) |
| 5 | Shell light brown, tergum with small furrow restricted to apical end | <i>Elminius adelaidae</i> Bayliss (South Australia) |
| | Shell translucent with red coloration, purple in field, tergum with concave articular margin, deep furrow | <i>Elminius erubescens</i> sp. nov. (South Australia) |
| | Shell buff red with cream ridges, tergum hatchet shaped | <i>Elminius covertus</i> Foster (NSW, Western Australia) |
| 6 | Shell pale brown with reddish brown bands between low ribs, tergum with spur longer than basiscutal angle | <i>Hexaminius foliorum</i> Anderson, Anderson & Egan (NSW) |
| | Shell greyish cream with darker radial bands, tergum with spur not longer than basiscutal angle | <i>Hexaminius popeiana</i> Foster (NSW) |

Discussion

The diversity of extant species, as well as fossil evidence, suggests that the Elminiinae originated in south-eastern Australia (Buckeridge 1982, 1984). The species present in South Australia are, with the exception of *Elminius modestus*, not found in NSW. The genus *Hexaminius* is not represented in South Australia and *Elminius covertus* is also absent.

South Australian barnacle populations are geographically isolated from the eastern States by a long expanse of coastline: from Robe to Cape Otway in Victoria, in which intertidal species are virtually absent (Womersley & Edmonds 1958). In South Australia there are extensive areas of coastline which are protected from oceanic waves in the gulfs which contain ideal habitats for *Elminius*. Speciation may have occurred in the variety of sheltered habitats which are available.

It is also possible that species from elsewhere along the southern coastline of Australia have been introduced. At present the distribution of *Elminius* species in other States has not been determined. The presence of *E. covertus* in Western Australia (Foster 1982) has been confirmed by Jones (1990). It is possible that it was introduced from eastern Australia. *E. modestus* may have been introduced from New Zealand (Foster 1982; Flowerdew 1984), but an electrophoretic comparison involving South Australian forms has yet to be done.

At present there is a large scale attempt to establish an oyster industry in South Australia using spat from Tasmania. This could lead to introductions of species not endemic to South Australia.

Two species of *Elminius* are extremely abundant in mangroves in South Australia, but their distributions do not overlap. *E. adelaidae* is found in the mangroves north of Adelaide whereas *E. placidus* is found in mangroves in the Spencer Gulf. The two gulfs have considerable differences in their marine invertebrate fauna (Shepherd 1983).

Only *E. adelaidae* utilises the leaves as well as the branches and pneumatophores. Anderson *et al.* (1988) have described a species *Hexaminius foliorum*, which is specialised for living on leaves. The adaptations they list as important for this species, which include thin shell, thick basal membrane, long elongated cirri and rapid cirral beating, are also found in *E. adelaidae*. Nevertheless, *E. adelaidae* grows to a much larger size, is found in other habitats and has a larger variety of cirral beating patterns, including the ability to hold the cirral fan fully extended. *E. placidus* has a more restricted range of cirral activity and lacks the ability to beat rapidly. The basal membrane is also thinner. Its thin shell and elongated body suggest a species adapted for very calm habitats, but not necessarily mangroves.

In New Zealand *E. modestus* is reported to live in mangroves (Moore 1944; Marton & Miller 1968). The present author has observed several spatfalls in mangroves near Adelaide, but they failed to persist. It is uncommon for *E. flindersi* to be found in mangroves and no *E. erubescens* were found in mangroves despite its abundance on rocks in the Adelaide region.

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EVALUATION OF EXTENSIVE ARID RANGELANDS: THE LAND CONDITION INDEX (LCI)

By ROBERT T. LANGE, BRENDAN G. LAY† & RODGER W. TYNAN†*

Summary

Lange, R. T., Lay, B. G. & Tynan, R. W. (1994) Evaluation of extensive arid rangelands: the land condition index (LCI). Trans. R. Soc. S. Aust. 118(2), 125-131, 31 May, 1994.

Social and historical circumstances that have given rise to rigorous new rangeland management legislation in South Australia are outlined. A program specified by the legislation is explained and described which will determine the condition of the 40 million hectares of arid rangeland in South Australia relative to criteria about sustainability and prevention and rectification of degradation. An objective assessment of average rangeland condition, the Land Condition Index (LCI) is introduced and results obtained by its use are illustrated and appraised.

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KEY WORDS. Arid zone, rangelands, Australia, vegetation, assessment, technique.

Introduction

The Pastoral Land Management and Conservation Act (1989) came into operation in South Australia in March, 1990, after years of public contention. It challenged the then Outback Management Branch of the South Australian Lands Department (as the responsible agency) with an immense, mandatory land assessment task within an 8-year deadline. In its combination of difficult features and its emphasis on sustainability, this task may have parallels in other arid parts of the world, where our procedures might, therefore, be applicable.

The particular combination of challenging features is a vast rangeland area (the size of Iraq or Somalia for example) poorly documented and difficult of access, to be assessed for the integrity of its vegetation and soils in detail, according to characteristics not accessible by remote sensing, using minimal time, staff and money.

We faced the further difficulty (given the limited amount of resources relative to the immense size of the task) that our assessments even of small tracts of land (a few hundred ha or so) would have to be capable of withstanding challenge and close scrutiny in a court of law.

This paper outlines (a) the historical and social context of the Act, (b) an approach (including a new index of land condition) which we have devised to help achieve what the Act requires and (c) some initial results obtained by application of the index.

Australian Background

Whether native inland Australian vegetation can ultimately withstand the impact of ungulate flocks and herds is yet to be determined. Since it evolved in total isolation from ungulates, it may prove unavoidably susceptible to the effects of large numbers of them. From prehistoric time until the mid-19th century, the inland arid regions of S.A. sustained only sparse Aboriginal nomadic hunter-gatherers. Due to lack of surface waters most vegetation probably experienced only very light grazing pressure, on average, by kangaroos alone. That regime changed "cataclysmically" (Adamson & Fox 1982) when Europeans colonised much of the country, tapped ground waters and introduced millions of ungulate stock and various feral animals, creating a sedentary grazing industry which now occupies 40 m ha (Fig. 1) and is mostly in the early part of its second century of operation.

The saying "Out of sight, out of mind" aptly summarises public and governmental attitudes to pastoral zone landcare throughout much of the industry's history (Lange 1983). Nearly all of South Australia's 1 m people dwell in the arable coastal regions and of these the vast majority live in and about Adelaide. Only a few hundred at any one time have had extensive pastoral zone experience. City-dwellers have only recently become better aware and more vocal about the arid zone, as tourism, wildlife protection, recreation and mining have increased.

Sheep stocking enterprises typical of the more southerly parts of the zone are protected from predatory dingoes by a special fence (the Dog Fence). Features include the subdivision of the rangeland into wire-fenced paddocks with water available for stock at fixed points, approximately fixed flock size year in, year out and a system of vehicular access tracks. This leads to the development of repeated drink-centred patterns of unequal flocktime distribution (piosphere pattern, Lange 1969, 1985; Andrew 1988) in which flocktime

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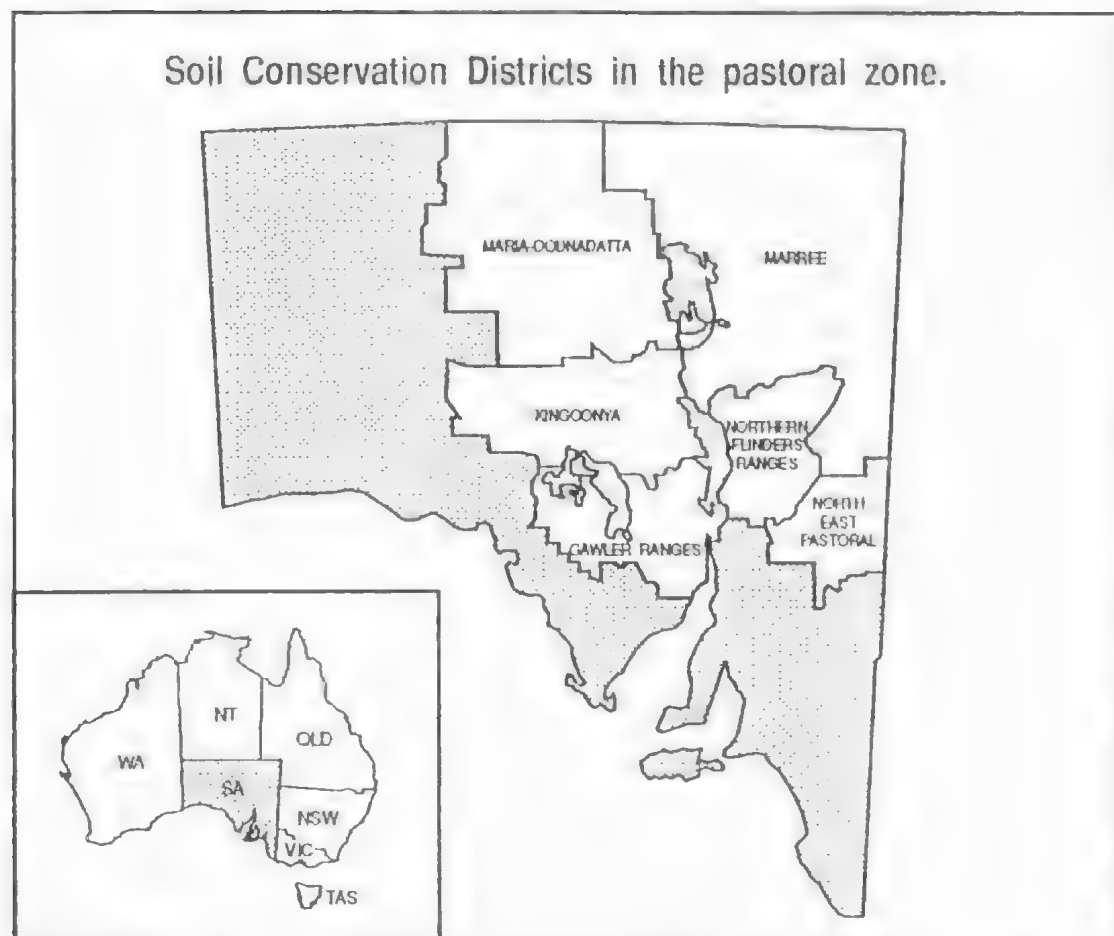


Fig. 1. The pastoral lease lands of South Australia, showing also their subdivision into Soil Conservation Districts.

concentrations can rapidly cause damage to the vegetation and soil, particularly during drought periods. The northerly extensions, exclusive to cattle, show the same patterns on a broader scale, with most pastoral properties there without internal fences.

Scientific and general literature, government inspectors' reports and the like show that from its inception onwards, this industry has caused great damage to the land, in some cases denuding the soil in just 2-3 decades (Dixon 1892; Waite 1896; Ratcliffe 1936; Pick 1944; Lay 1979). This was of public concern particularly in the 1930s when the issue of soil erosion was topical worldwide (Jacks & Whyte 1939) and has subsequently remained a problem. Half a century later in the 1980s, government administration again publicly conceded that some pastoralists were still failing to meet landcare obligations and that land degradation from overstocking and feral animal pests was extensive¹. In an attempt to accommodate all interested parties, the Pastoral Land Management and Conservation (PLMC) Act was finally passed in 1989.

This Act is profoundly different from earlier South Australian pastoral laws in its great emphasis on resource protection. It is, in fact, unequivocal landcare legislation (in some ways setting scarcely-attainable ideals of landcare perfection) but it also provides provisions for grazing industry protection and appeal. How these opposites will be reconciled in practice is yet to be shown.

Of special relevance to this paper, the new Act gave the Minister of Lands greatly increased scientific and technical responsibilities. The administration of the Act is delegated to the Pastoral Board (whose membership reflects major interests in pastoralism and conservation) but the technical tasks must be carried out by the Pastoral Management Branch. Of these tasks, this paper refers to the requirement for vegetation assessment. This immense task, which the Act requires

¹South Australian Government, Lands Department (1981). The administration, management and tenure of South Australia's Pastoral Lands. Interdepartmental Report (Chairman: J. Vickery, Lands Department).

to be carried out within eight years and at 14-year intervals thereafter, relates to 40 m ha of the rangelands and is to specify the condition of the land according to criteria derived from the Objects of the new Act. These effectively require that the whole area be directly inspected by teams of trained assessors on the ground. As is usual where a large and complicated task must be accomplished piecemeal by different teams, objective, standardised procedures need to be adopted to ensure that the findings of any assessment are independent of the particular team employed. The development of the index and training procedures described below is an attempt at such standardisation.

The Legal Stipulations about Assessment

In South Australia's non-arable inland regions a pastoral lease is the only form of tenure than can be granted over Crown (government) land that is to be used for long-term grazing purposes; a pastoral lease cannot be granted or extended without an assessment of the condition of the land first having been made (PLMC Act, 1989, Sec. 20, 25). This is why the assessment program is urgent and crucial. The pastoral industry is awaiting the issuing of new leases, specifying new stocking limits and other conditions consequent upon these assessments.

Section 6 of the PLMC Act states that such assessment of the condition of the land must be thorough, must include an assessment of the capacity of the land to carry stock, must be conducted in accordance with recognised scientific principles and must be carried out by persons who are qualified and experienced in land assessment techniques.

The further meaning of assessment derives directly from relevant Objects of the PLMC Act (Sec. 4) which are: (a) to ensure that all pastoral land in the State is well-managed and utilised prudently so that its renewable resources are maintained and its yield sustained and (b) to provide for (1) the effective monitoring of the condition of pastoral land, (2) the prevention of degradation of the land and its indigenous plant and animal life and (3) the rehabilitation of the land in cases of damage. The Minister is expressly charged (PLMC Act, Sec. 5) with the duty of acting consistently with and in furtherance of those Objects. Assessment pursuant to the Act (that is the process of obtaining scientifically based answers to the Objects posed as questions, viz., Is this pastoral land well-managed and utilised prudently so that its renewable resources are being maintained and its yield sustained? Is degradation of the land and of its indigenous plant and animal life being prevented? Is there degradation which requires rehabilitation? Has effective monitoring of the condition of the land been provided? What is the capacity of the land to carry stock consistently with answers to the foregoing questions?

Since "degradation" is defined (PLMC Act, Sec. 3) as a decline in the quality of the natural resources of the land resulting from human activities, some of the implications arising from the Objects are immediately apparent. For instance, the conventional rangelands dogma that the desirable condition of the vegetation is that which feeds most stock is potentially denied by this legislation. The optimal condition instead is that where indigenous plant and animal life retain their prepastoral integrity while as far as possible sustaining a viable pastoral industry. Appreciation of this difference is crucial in developing the condition index outlined below and it will be further examined in the Discussion.

That the answers to these assessment questions are meant to be taken seriously is made plain in many parts of the PLMC Act including Sec. 43 for example, a Section excluded from the appeal provisions (Sec. 54, 55). Section 43 makes it clear that the Pastoral Board should require the removal of stock from an area not only if it believes that the land has been damaged but also if the Board considers that the land is likely to suffer damage.

Essential Preliminaries to Assessment

It should be noted here that the assessment program as developed consists of two parts viz., the lease-based Land Condition Index determination (the subject of this paper) and a network of paddock-based photo-monitoring sites. These latter sites, with vegetation and soils data collected, form the base line for the assessment of future trends in each paddock.

Access and Sampling

Any thorough assessment of a station or lease in accordance with recognised scientific principles (Sec. 6 of the PLMC Act) should employ many independent samples in an effort to achieve a picture which is as balanced and equitable as is practicable. In practice, sampling falls somewhere between systematic and random, as in the way the industry itself informs potential buyers about the contents of a bale of wool, for example, where the sample is from an arbitrary grab. In sampling station condition, reliance is usually placed upon the pastoralist's system of vehicle access tracks to spread samples throughout the overall area. Then, to avoid possible observer bias, samples are drawn by strict restricted-random processes from what is track-accessible. There are some obvious consequences of such sampling but they are more academic than practical and there is no evidence that they significantly affect comparisons. All well-developed pastoral land has adequate watering points and a network of access tracks linking them. Thus there is a higher than random likelihood of sampling closer to water, and a correspondingly reduced likelihood at intermediate ranges, than would result on random

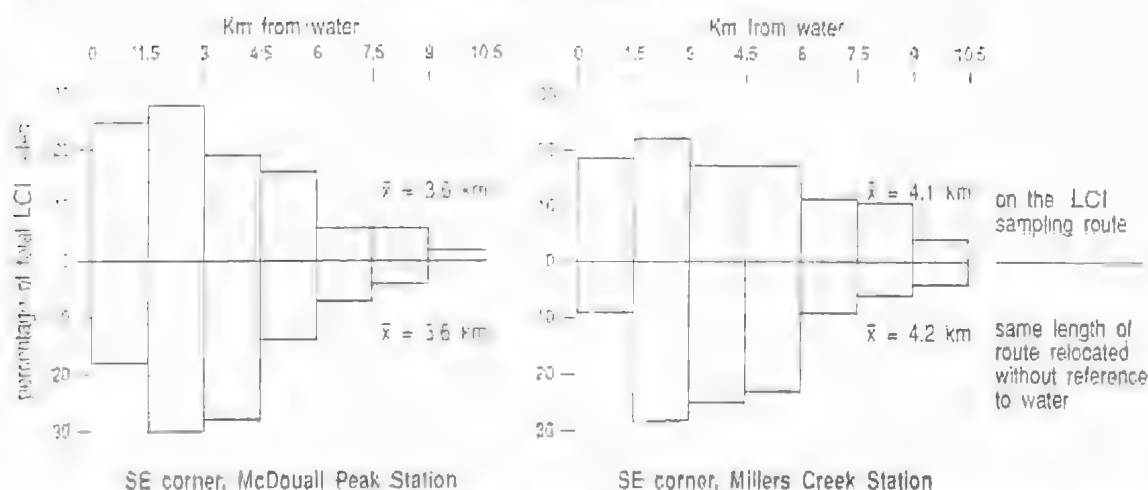


Fig. 2 Histograms showing the percentage of sampling points at various distances from water points on the access tracks (above) and when the same track-grid is offset from water-points (below).

tracks. This effect is consistent from station to station (Fig. 2) and can always be taken into account.

Recognition of Vegetation Type and Component

The next essential of the assessment procedure is that the assessment team member, at any sample point, must recognise which of the many different vegetation types is represented and, of that type, which of the various sub-types called components. In practice this ability comes from instruction manuals and field training provided by us, as experienced team members, who have a collective 60 years of botanical work experience in the region to draw upon. Learning is simplified by restricting consideration to manuals drawn up for one Soil Conservation District at a time, thus reducing the immediate diversity to be handled. The assessment teams then attack the task by completing assessments of one District before re-calibration and assessment of the next District and so on.

We write keys for the identification and separation of the vegetation types and components in each district, with sets of criteria to distinguish condition classes (see below) and we illustrate the resulting manuals with extensive colour photo-guides. All teams are then trained en bloc (in extended field calibration exercises) to achieve a uniform, consistent interpretation of all criteria.

All main diagnostic criteria refer to perennial plants, rather than to ephemerals which appear only after significant rainfall. The main reason for reference to perennials is that they embody the drought fodder reserves of the rangeland as well as being the reliable buffer against wind erosion. There are a few places, particularly in northern cattle rangelands, that lack perennial vegetation sufficient for present purposes; these will be treated in separate ways.

TABLE 1. Vegetation type and component used in LCI.

Type	Component
Chenopod shrublands	<i>Atriplex vesicaria</i> - <i>Maireana astrolirica</i> treeless plains
Woodlands with grassy understorey	<i>Acacia aneura</i> - <i>A. ramulosa</i> -grass sp. on deep sands.

The level at which types and components in general are distinguished is indicated by the examples giving the names of predominant species in Table 1.

Condition Classes

Arguments about non-linear 'state and transition' models of rangelands dynamics notwithstanding (Westoby *et al.* 1989), experience of S.A. rangelands shows that in general any component can be placed into one or other of three condition classes viz., Class 3, with the original stock-palatable perennial species still present and reproducing, Class 2, with the original palatable perennial species being eliminated (if grasses or low shrub species) or lacking all juveniles (if large long-lived perennials) and with replacement by much less-palatable perennial species including weeds or by ephemerals and Class 1, with all palatable perennial species eliminated except old trees, unpalatable species heavily pruned, many weeds present or, in some cases, the integrity of plant cover totally destroyed. It has of course been demonstrated for nearly 60 years that deterioration to Class 1 goes hand in hand with the onset and rapid acceleration of soil erosion (Ratcliffe 1936; Jacks & Whyte 1939; Pick 1944; Lay 1979).

The advantage of distinguishing only three classes is that only two sets of separation-criteria are then required i.e. separating Class 3 from Class 2 and Class 2 from Class 1. Obviously, it is easier to train all

assessment teams to absolute consistency when they have to apply only two sets of separation criteria to describe the condition of some given vegetational component instead of three, four or more sets. Contrary to what at first sight might seem to be the case, this restriction to just three condition classes in no way limits the general sensitivity of inter-lease comparisons. When the condition of two leases is to be compared, the sensitivity of the index of comparison depends instead on a sufficient number of samples plus the use of weighted averages, as will be demonstrated. So, in specifying arbitrary but consistent criteria for the separation of condition classes, counts can be avoided in favour of absolute differences. Regarding the *A. vesicaria*-*M. astrotricha* component of the chenopod shrublands, for example, the main criterion for separating condition Class 3 from condition Class 2 is the elimination of *A. vesicaria* (a grazing-susceptible species of the original palatable perennial component). Condition Class 1 is distinguished from Class 2 by loss of *M. astrotricha*, a palatable but more grazing-resistant perennial. Taking the example of the *Acacia aneura*-*A. ramulosa*-grass sp. component of the woodlands with grassy understorey, condition Class 2 involves loss of all *A. aneura* regeneration, appearance of a distinct browse line on old trees, elimination of the most palatable perennial grasses (e.g. *Monachather paradoxa*) and severe pruning, at least, of palatable shrubs (e.g. *Eremophila latrobei*). Similar sets of criteria have been adopted to distinguish condition classes of all vegetational components of all types in the rangelands, supported by photographic examples of these classes.

Training

An essential for condition assessment conducted piecemeal by different teams, using this method, is a full scale combined field-training exercise. The Soil Conservation District to be assessed is traversed to intersect all vegetation types and components. At stop after stop on this traverse, samples are assessed by the party as a whole, according to the manual, until all questions have been resolved on the spot, guaranteeing uniformity of interpretation. Only then are the different teams allocated their particular shares of the district workload and the actual assessments conducted.

Predetermination of Sampling Points

Using available maps of station tracks, the assessment sampling route is pre-selected for best systematic coverage and the total length involved is calculated using an opisometer. That length is then divided into 100 equal parts within each of which a precise stopping-point is drawn at random. The results are then programmed into a computerised trip-meter (Halda Instrument Co.) mounted in the access vehicle, which then signals the stops. This guarantees restricted-random sampling of the route.

Assessment and LCI Calculation

Field teams comprising a scientific officer and a technical officer operate self-contained 4-wheel drive expeditionary vehicles equipped for remote area operations, including radio communications. Navigation is by reference to available maps and satellite imagery using a vehicle-mounted GPS unit. At each sample site (of which the trip meter sounds prior warning and displays a count down to 10 m), the reference is made to the 50 m-square plot located immediately beyond a line parallel to the direction of vehicular travel, 10 m offset from the left side of the vehicle. The sample within this plot is rated according to vegetation type, component and condition, is photographed and the data are recorded. At the conclusion of sampling, the station land condition (LCI) is calculated as in the hypothetical example in Table 2.

TABLE 2. Example of calculation of LCI (station land condition).

Condition Class	Percentage of samples	Multipher		Totals
3	50	$\times 3$	=	150
2	30	$\times 2$	=	60
1	20	$\times 1$	=	20
	100			230
		LCI	=	2.30

Note that this index has limits of 1.00 (the whole station in "degraded" condition) and 3.00 (the whole station in "undegraded" condition). Actual stations have values between these limits. Note also that the index, once calculated, is not to be interpreted mechanistically but instead is used for first-order sorting of stations according to condition. Other evidence and data collected independently about each station are then taken into account. Stations can be compared directly by the LCI only where they involve similar pasture types and components in similar proportions.

The Nature of Initial Results

Assessment teams obtained first results during 1991 from the Kingoonya Soil Conservation District of South Australia using 19 stations. Fig. 3 makes a comparison between the LCI scores of lands making up the stations in this district and the maximum stocking permitted on them by the provisions of existing lease documents. As can be seen, no station attains the ideal of the Act (all samples in Class 3). Instead, stations range very widely in condition, from as low as 160 up to 270, with an average of about 200. This low average score would imply that maximum stocking allowances will have to be reduced, on average, to enable some progress with

the rehabilitative process prescribed by the PLMC Act. As can also be seen, there is no consistent relationship between the present condition of stations and the maximum stock that they are currently permitted to carry. This is in contradiction to the Objects of the legislation which imply clearly that stocking, if it is to be intense, must go hand in hand with the maintenance of a high LCI score.

From the descriptions above it can be seen that the LCI provides a comparative assessment of stations on standardised criteria derived specifically from the Objects of the Pastoral Land Management and Conservation Act, synthesising an overall picture from data provided by means of teams of which none has seen more than a few of the total stations. It thus fulfils its design purpose and can deliver defensible comparative assessments to the Pastoral Board, which has the task of finalising judgments affecting stocking.

Fig. 3 shows the crucial difference between station country as perceived according to the Objects of the Act on the one hand and as perceived through "pastoral production" eyes on the other. For example, station land occupied by salt flats with inedible samphires

(Chenopodiaceae tribe Salicornae) vegetation might score a perfect 3.00 on the LCI scale, for completely satisfying the landcare Objects of the Act, while being intrinsically useless for pastoral production whereas overgrazed and denuded lands (e.g. chenopod shrublands reduced to ephemeral grasslands) of very low LCI score might earn the pastoralist substantial profits as a result of high animal production. The aim of the Act where LCI scores are low is to arrest decline and then reverse it into a long-term trend of ascending LCI scores as a first priority. Any stocking of the lands has to be commensurate with that and be a secondary consideration.

Two major advances in ecological data-collection arise from the LCI sampling program. Since the distribution of the sampling sites is known, and is as close to an even scatter as can be achieved, the data yield estimates of the proportions of the district that are occupied by the various types and components of the rangelands vegetation as well as distribution details. Further, since the condition of the component at each site is recorded, the condition-profile of each rangelands vegetational component can be specified,

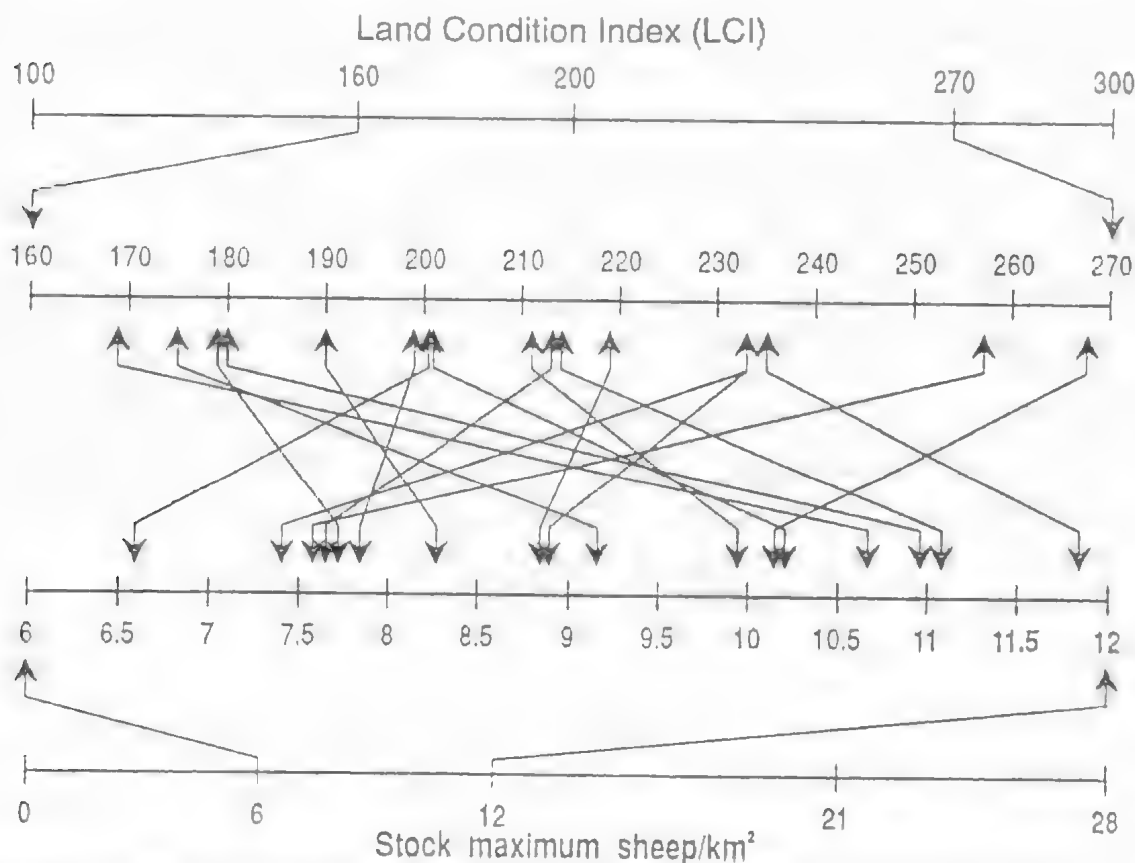


Fig. 3. The prevailing mismatching between stocking allowances amongst leases of the Kingoonya Soil District, South Australia.

revealing the relative degree to which the different types have been degraded. This is important management information. It is upon the basis of data such as these that the Pastoral Land Management and Conservation Act must operate and without which its administration cannot address its legally-stipulated imperatives.

Discussion

Well-reasoned technical prescriptions for landcare in the State's pastoral zone have been available for almost a century. Waite (1896) aimed for a balance between offtake and sustainability via a well-reasoned ecological argument involving land and flock subdivision, waterpoint multiplication, nutrition of lactating ewes, the distances sheep walk, drought strategy, deferred grazing, spelling and economics. Waite's key principles have been firmly linked with good landcare by Lay (1979) on the basis of long-term studies. The most recent managerial prescription (Stafford-Smith & Morton 1990) is little different in principle from the first (Waite 1896) so it is not deficiency of management advice that explains a century of ongoing degradation.

From initial experience with the LCI it now seems probable that most stations in South Australia will fall short of the land condition ideal of the new Act. This means that reclamatory, rehabilitatory action will predictably be required which involves recommendations for reduced stocking levels. We believe that those stations managed in closest accord with the Act (highest LCI) should retain for the present their existing stocking allowances and act as benchmarks for other stations with similar vegetation types but lower indices. These other stations should be given lower stocking limits while rehabilitation programs are initiated. One reason for not recommending stocking allowances higher than at present in any instance (even on stations with highest LCI) is due to a feature of the index itself. In order to guard against likely accusations that the assessment scoring procedures are too severe, they were structured in favour of high LCI scores rather than otherwise. For example, downgrading a saltbush (*Atriplex vestitoria*) shrubland from condition Class 3 to 2 is forestalled while just a scattering of saltbush remains, even though the ungrazed density was many thousand/ha. Thus where even the best-preserved vegetation in an area scores less than the ideal, there is no full compliance with the sustainability notion central to the Act.

In its initial considerations of the first leases assessed by this method in the Kingoonya Soil Conservation District, the Pastoral Board has been reluctant to adjust leases with low LCI scores unless these scores can be directly attributable to current management

Rather, it has indicated it would await an indication of trend from permanent photo-monitoring sites set up at the time the LCI is determined.

Of the many further points that might be made, the one warranting most emphasis here is that the LCI and associated procedures have to be taken against the backdrop of the stringencies, pressures and urgencies that attend it. Those who might regard it as hasty (compared with what has been attempted in some other Australian States) should recall the timeframe. The whole rangelands (40 m ha) must be by law assessed in eight years; this is a formidable and costly task.

Ultimately, however, landcare in the zone will depend not on the assessments but on the determination with which executive government uses the assessment information to ensure that more sustainable land management practices are adopted in our arid rangelands.

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A SMALL STHENURINE KANGAROO FROM A PLEISTOCENE CAVE DEPOSIT, NULLARBOR PLAIN, WESTERN AUSTRALIA

*By G. J. PRIDEAUX**

Summary

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Key Words: sthenurine kangaroo, *Simosthenurus maddocki nullarborensis* ssp. nov., *Simosthenurus maddocki maddocki*, Lindsay Hall Cave, Nullarbor Plain, Pleistocene, geographic dwarfing.

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Introduction

In April 1991, a recently collapsed opening to a limestone cave was discovered by members of the Western Australian Plane Caving Group on Madura Station, northwest of Madura Pass on the Nullarbor

Plain (Fig. 1). Fossil material was removed from the cave, named Lindsay Hall Cave, during exploration in September 1991 and April 1992. Several cranial fragments belonging to a medium to large size sthenurine, and a very small partial left maxilla were recovered. This latter specimen represents a new form smaller than any sthenurine previously described from the Pleistocene. It most closely resembles *Simosthenurus maddockii* Wells & Murray, 1979 from eastern Australia with which it is compared. This paper describes the new sthenurine.

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Fig. 1. Deposits yielding *Simosthenurus maddockii* in southeastern Australia.

Material and Methods

The material is housed in the Western Australian Museum, Perth (WAM). Mensuration, dental terminology and nomenclature follow Tedford (1966). As the homology of premolar cusps is currently being re-examined by Prof. David Ride (pers. comm.), they are referred to here as an anterior labial cusp, posterior lingual cusp, etc. All measurements are in millimetres. Abbreviations: L = length; AW = anterior width protoloph(id); PW = posterior width metaloph, hypolophid; AH = anterior crown height, labial side; PH = posterior height; n = sample size. Note crown height measurements are heavily dependent on degree of enamel wear.

Systematics

Order: DIPROTODONTIA Owen, 1866
 Suborder: PHALANGERIDA Aplin & Archer, 1987
 Superfamily: MACROPODOIDEA Gray, 1821
 Family: MACROPODIDAE Gray, 1821
 Subfamily: STHENURINAE (Glauert, 1926)
 Genus: SIMOSTHENURUS Tedford, 1966

Simosthenurus maddocki maddocki
 Wells & Murray, 1979
 FIGS 1, 5

Holotype: SAM P16999, a near complete juvenile skull collected from Victoria Fossil Cave, Naracoorte, South Australia. Diagnosis, description and comparison of nominotypic form of *S. maddocki* is provided by Wells & Murray (1979). This subspecies is also recognised from Greenwater Hole Cave, near Tantanoola in South Australia (Pledge 1980), Bingara, Wombeyan Caves and Mt Fairy in New South Wales (Flannery & Hope 1983), and Lancefield in Victoria (pers. observation). Age of type locality is late Pleistocene (Wells *et al.* 1984).

Simosthenurus maddocki nullarborensis ssp. nov.
 FIGS 1-5

Holotype: WAM 92.9.8, a partial left juvenile maxilla collected from Lindsay Hall Cave, near Madura, Nullarbor Plain, Western Australia (31°35'S, 126°40'E). Collected in September 1991 by Wendy Binks and Katherine Crisp, Western Australian Plane Caving Group. Age of type locality is ?late Pleistocene.

Diagnosis: Maxilla smaller than *Simosthenurus maddocki maddocki* Wells & Murray, 1979 and *Sthenurus gilli* Merrilees, 1965; molars low crowned, very similar in morphology to *S. m. maddocki*, but smaller. Molars possess very fine enamel crenulations with lophs notably convex anteriorly. P³ very small, narrow to tapered anteriorly, but inflated posteriorly.

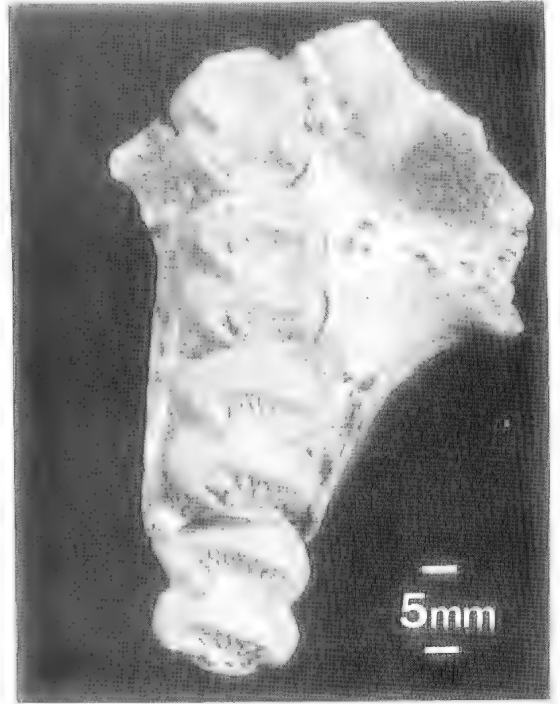


Fig. 2. Stereopair of *Simosthenurus maddocki nullarborensis* ssp. nov. left maxilla (WAM 92.9.8, holotype) in occlusal view.

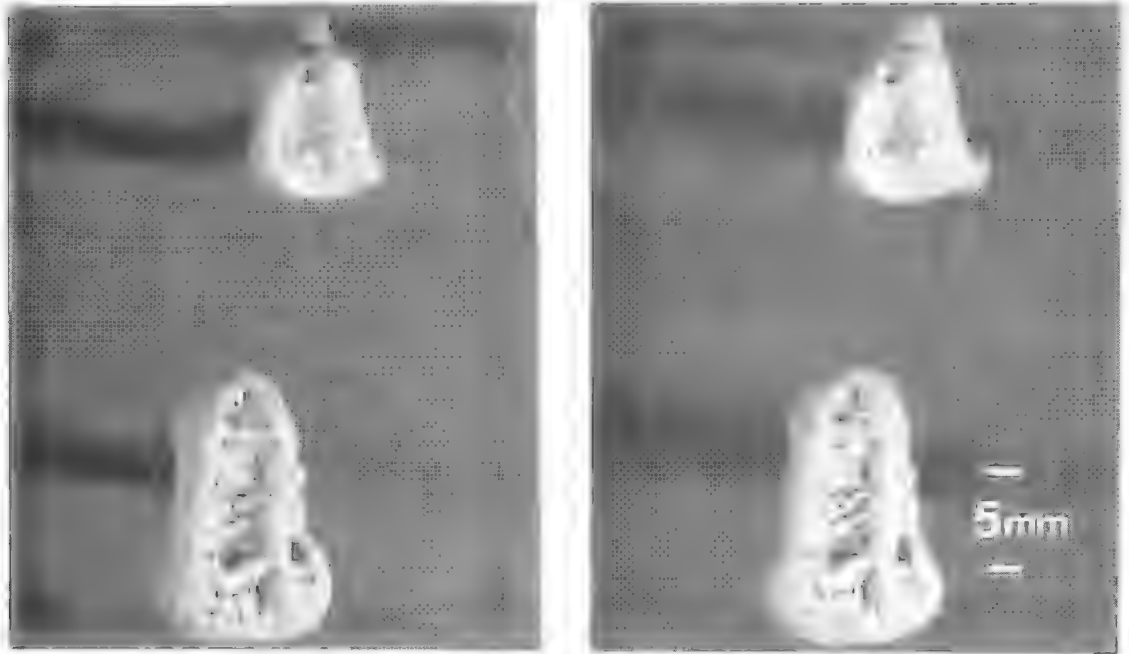


Fig. 3. Stereopairs of *Simosthenurus maddocki nullarborensis* ssp. nov. left P^2 , top, and P^1 , bottom, (WAM 92.98, holotype) in occlusal view.

Description of holotype: Maxilla (Fig. 2). Fragmentary nature of specimen has resulted in preservation of very few non-dental characters suitable for description or comparison. Palatine vacuities appear to have extended anteriorly to level of dP^1 anterior loph. Only base of masseteric process preserved in holotype making an estimation of size difficult. Posterior aspect of buccinator muscle scar is laterally wide.

Dentition (Figs 2-5, Table 1). Includes P^2 , dP^3 , M^{1-3} , excavated P^1 , with teeth exhibiting only beginning wear.

P^2 : Very small with relatively high labial crest containing prominent anterior labial cusp and small cuspsules posteriorly. Transverse ridge joining labial and lingual posterior cusps encloses posterior basin. Fine transverse ridgelets occupy longitudinal basin, with anteriormost slightly larger and dividing off small anterior basin.

dP^1 : Completely molariform, wider across posterior loph than anterior loph, and smaller than succeeding molars.

P^1 : Posterior third of P^3 inflated both labially and lingually. Posterolabial styler cusp is well developed but does not attain height of posterior labial cusp. Labial crest divided into three cuspsules bordered at both extremes by prominent anterior and posterior cusps. Transverse ridge leading halfway into longitudinal basin from labial crest slightly overlaps with small ridge descending across from lingual crest

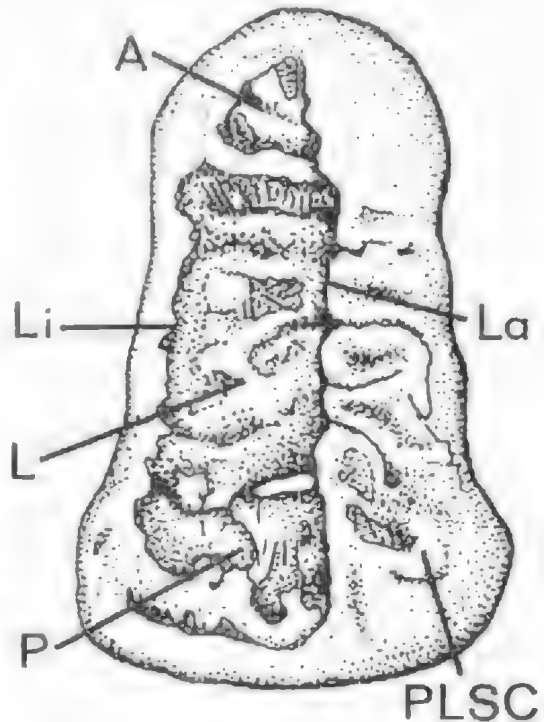


Fig. 4. Drawing of the holotype P^1 of *Simosthenurus maddocki nullarborensis* ssp. nov. A, anterior basin; P, posterior basin; L, longitudinal basin; La, labial crest; Li, lingual crest; PLSC, posterolabial styler cusp. (Length = 13.3mm).

to form anterior border of posterior basin. Small anterior basin separated by transverse ridge descending lingually from prominent anterolabial cusp to lingual counterpart. Ridge appears to have formed from unification of two smaller ridges descending transversely from each anterior cusp.

M¹⁻⁴: Molars increase in length and width from M¹ to M³ (M⁴ not preserved). Respective widths across proto-loph and meta-loph in M¹ are identical. In M², proto-loph wider than meta-loph, and in M³ wider again. Molars low crowned with lochs notably convex anteriorly. Very fine crenulations on molars are extensive, slightly coarser on posterior side of meta-loph. Anterior cingulum well developed, but not especially broad. It extends anteriorly from tip of paracone, then labially across almost entire width of proto-loph. Low, weak postproto-crista extends posterolabially from protocone and meets with very small crest originating from meta-loph, forming a crista obliqua. Lingual to this structure, a deep fossette is present in median valley. Labially, a notch is formed between well developed postpara- and premetacristae. Posterior cingulum broad and formed by fine posthypo-crista descending posterolabially, then labially across back of molar, and overlapping with less prominent postmetacrista.

Paratype: WAM 92.12.7, a singular, unassociated P¹

from Lindsay Hall Cave. Collected in April 1992 by Lindsay Hatcher, Western Australian Plane Caving Group.

Variation: It is only possible to get an impression of variation within *S. m. nullarborensis* by comparing the P³ of WAM 92.9.8 and WAM 92.12.7. They differ slightly in size, namely length and posterior width, but more noticeably in morphology. Whereas the posterior third of the P³ in WAM 92.9.8 is inflated both labially and lingually, there is only a lingual inflation in WAM 92.12.7 (Fig. 4). This is due largely to the reduced development of the posterolabial styler cusp in WAM 92.12.7 compared to the holotype. This is an especially variable character in other sthenurines, including *S. m. maddocki* and *S. occidentalis*, and probably also represents intrasubspecific variation in *S. m. nullarborensis*. Other notable differences between the premolars are the lateral tapering present in WAM 92.9.8, where the tooth becomes more narrow anteriorly than WAM 92.12.7, and the incipient development of the anterior cingulum in WAM 92.12.7 compared to WAM 92.9.8. Intraspecific variation in premolar morphology is common in all sthenurine species for which numerous individuals are known (pers. observation).

Comparison with other taxa: Clearly, the skull of *S. m. nullarborensis* was very small even considering

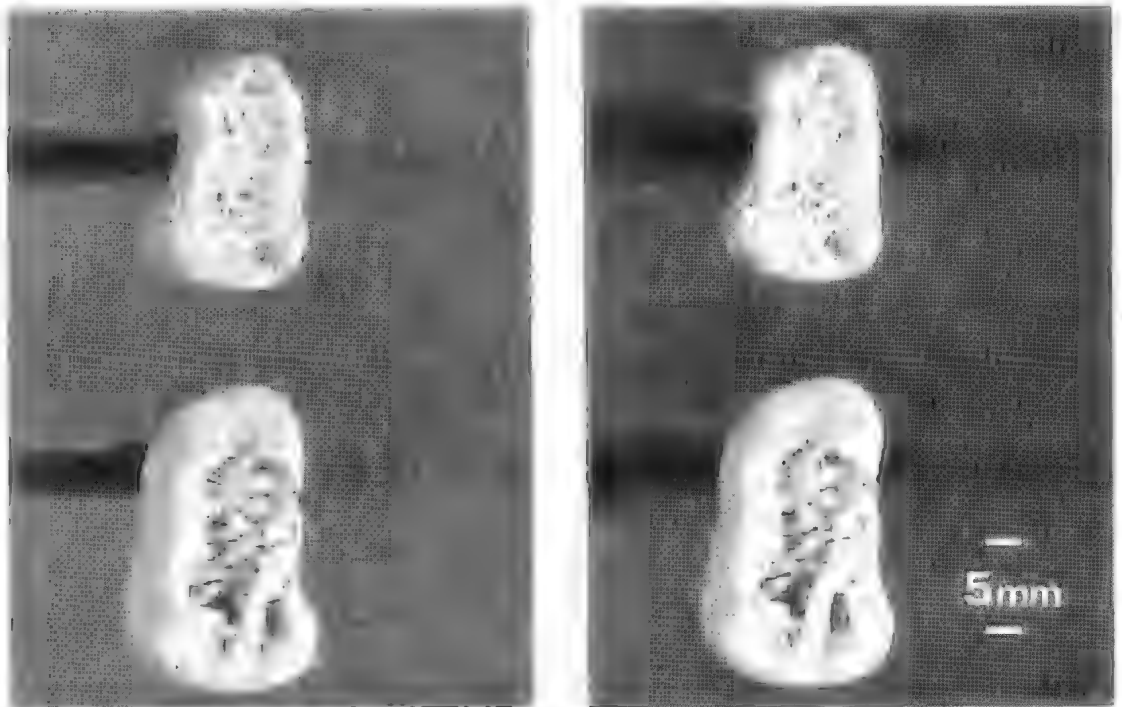


Fig. 5. Stereopair of *Simosthenurus maddocki nullarborensis* ssp. nov. P³, top (WAM 92.12.7, paratype), and typical *Simosthenurus maddocki maddocki* P³; bottom (SAM P27752), in occlusal view.

the difficulty involved with interpreting skull size from fragmentary juvenile specimens. The preserved maxillary region is smaller in every respect than similarly-aged individuals of *S. gilli*, previously recognised as the most diminutive extinct sthenurine. It is much smaller than similarly-aged *S. m. maddocki*. Anterior extension of the palatine vacuities and the morphology of the buccinator muscle scar in *S. m. nullarborensis* are both similar to *S. m. maddocki*.

The P^2 and P^3 of *S. m. nullarborensis* are considerably smaller than *S. m. maddocki* (Table 1). Although only two P^1 specimens were available to conduct one-tailed t-tests, both length ($t=3.3$, $P=0.09$) and anterior width ($t=3.0$, $P=0.01$) for *S. m. nullarborensis* fell significantly outside of the known range of *S. m. maddocki*. As with the maxilla, they are smaller in size than those of any sthenurine. Based on the comparison of mean length and width

measurements, they are 24% smaller than *S. m. maddocki*.

S. m. nullarborensis and *S. m. maddocki* differ in several morphological features of the P^1 . The posterolabial styler cusp is less prominent in *S. m. nullarborensis*, especially in WAM 92.12.7. Neither specimen possesses a styler cusp which attains the height of the posterior labial cusp, contrasting *S. m. maddocki* in which the height of the styler cusp consistently exceeds that of the posterior labial cusp. In *S. m. maddocki* the labial crest is divided into either two or three cusps between the larger anterior and posterior labial cusps. Both *S. m. nullarborensis* specimens possess three cusps but a similar variation in number could also occur in this subspecies. In the holotype P^3 the anterior basin is well formed and separated from the longitudinal basin by a transverse ridge (Fig. 4). This structure is not present

TABLE 1. Cheek teeth dimensions of *Simosthenurus maddocki nullarborensis* sp. nov., *S. m. maddocki* and *S. gilli* [mean (standard deviation) (observed range)]

Tooth	Species	L	AW	PW	AH	PH	n
P^2	<i>S. m. nullarborensis</i>	7.0	4.9	5.7	5.5	5.5	1
	<i>S. m. maddocki</i>	9.2 (0.15) [9.0-9.4]	6.2 (0.53) [5.8-7.1]	7.3 (0.51) [6.7-8.1]	6.3 (0.49) [5.7-6.9]	6.2 (0.59) [5.7-6.9]	5
	<i>S. gilli</i>	10.0 (0.31) [9.6-10.5]	7.4 (0.21) [6.7-7.5]	8.9 (0.17) [8.6-9.1]	6.5 (0.23) [6.4-6.9]	6.7 (0.36) [6.3-7.3]	7
dP^3	<i>S. m. nullarborensis</i>	8.5	7.5	8.2	4.9	4.9	1
	<i>S. m. maddocki</i>	9.8 (0.11) [9.6-9.6]	8.7 (0.24) [8.4-9.0]	9.0 (0.36) [8.6-9.6]	5.0 (0.31) [4.6-5.5]	4.9 (0.24) [4.6-5.2]	7
	<i>S. gilli</i>	9.2 (0.21) [9.0-9.6]	9.2 (0.26) [8.9-9.6]	9.6 (0.32) [9.2-10.2]	4.9 (0.35) [4.3-5.3]	5.2 (0.23) [4.9-5.5]	11
P^3	<i>S. m. nullarborensis</i>	12.5 (1.13) [11.7-13.3]	5.8 (0.14) [5.7-5.9]	8.0 (0.71) [7.5-8.5]	6.5 (0.71) [6.0-7.0]	5.9 (0.21) [5.7-6.0]	2
	<i>S. m. maddocki</i>	16.0 (0.59) [15.3-17.0]	8.1 (0.51) [7.5-9.0]	10.1 (0.56) [9.3-11.1]	8.3 (0.30) [7.7-8.6]	7.7 (0.52) [7.1-8.6]	8
	<i>S. gilli</i>	16.1 (0.63) [15.2-17.1]	9.2 (0.54) [8.0-9.8]	11.4 (0.72) [10.2-12.8]	9.8 (0.98) [8.0-10.8]	9.8 (0.88) [8.3-10.8]	11
	<i>S. andersoni</i>	15.5 (0.53) [14.8-16.5]	7.7 (0.38) [7.2-8.2]	9.5 (0.38) [9.0-10.3]	9.4 (0.46) [8.9-10.0]	9.4 (0.68) [8.7-10.5]	8
M^1	<i>S. m. nullarborensis</i>	9.4	8.7	8.7	4.8	4.9	1
	<i>S. m. maddocki</i>	10.8 (0.29) [10.3-11.2]	10.1 (0.24) [9.7-10.5]	10.1 (0.44) [9.4-10.9]	5.3 (0.37) [4.8-5.7]	5.2 (0.39) [4.4-6.0]	9
	<i>S. gilli</i>	10.3 (0.51) [9.3-11.0]	10.2 (0.34) [9.6-10.7]	10.0 (0.33) [9.4-10.5]	5.5 (0.59) [4.3-6.2]	5.9 (0.54) [4.8-6.6]	11
M^2	<i>S. m. nullarborensis</i>	10.1	9.2	8.9	5.5	6.0	1
	<i>S. m. maddocki</i>	11.2 (0.21) [10.9-11.5]	10.8 (0.38) [10.5-11.6]	10.3 (0.34) [9.9-10.7]	5.5 (0.45) [4.9-6.2]	5.5 (0.47) [4.9-6.4]	7
	<i>S. gilli</i>	11.0 (0.49) [10.3-11.9]	10.5 (0.44) [9.9-11.0]	10.2 (0.36) [9.6-10.8]	6.1 (0.39) [5.6-6.7]	6.6 (0.33) [6.2-7.0]	11
M^3	<i>S. m. nullarborensis</i>	10.2	9.6	8.8	4.7	4.5	1
	<i>S. m. maddocki</i>	11.4 (0.29) [11.0-11.7]	11.1 (0.45) [10.5-11.9]	10.1 (0.48) [9.5-10.7]	5.7 (0.37) [5.0-6.2]	5.5 (0.38) [5.0-6.0]	7
	<i>S. gilli</i>	11.6 (0.46) [10.8-12.2]	10.7 (0.48) [10.0-11.6]	10.3 (0.50) [9.6-11.2]	6.2 (0.66) [5.5-7.8]	6.5 (0.68) [5.5-7.9]	11

in *S. m. maddocki* where inward curving of the anterior extremes of the labial and lingual crests occurs (Fig. 5). These often do not meet and result in an anterior basin which is very poorly designated or completely absent. A more intermediate condition is observed in WAM 92.12.7.

Complete molarisation of the P^3 's is characteristic of all sthenurines. Likewise, the increase in molar length and relative changes in widths along the tooth row in *S. m. nullarborensis* are typical of most species. Molar morphology is very similar to *S. m. maddocki*, making them readily separable from the similarly-sized *S. gilli*, which possesses a larger crista obliqua and less extensive fine enamel crenulations. Therefore, upper molars of the subspecies are separable on size only, with measurements of the *S. m. nullarborensis* molars approximately 13% smaller than mean values for *S. m. maddocki*.

Discussion

Although some doubt existed initially over which taxonomic rank should apply to the Nullarbor form, morphological similarity to nominotypic *S. maddocki* precluded a specific separation. Designation of fossil subspecies has previously been made in reference to dwarfing macropod lineages (Marshall & Corruccini 1978; Dawson & Flannery 1985). They are an effective form of recognising clear-cut temporal or geographical variants within a species. Size reduction in P^3 and molar dimensions (24% and 13% respectively) from *S. m. maddocki* to *S. m. nullarborensis* is comparable to that observed by Marshall & Corruccini for other medium to large-sized macropods from the Pleistocene to Holocene. They concluded that resource limitations probably accounted for dwarfing in these macropods and *Sarcophilus harrisii*. Dwarfing is commonly observed in island populations contemporaneous with large mammal populations on the mainland (Londrino

1985). A similar effect between mainland regions caused by climatic unpredictability, which today typifies the Nullarbor Plain, may also have been significant in the Pleistocene environment, perhaps leading to size reduction in *S. m. nullarborensis*.

Interestingly, analysis of size variation in *Thylacynus cynocephalus* from the Nullarbor Plain (Lawry 1972) did not statistically separate (as a subspecies) the population sample from larger *T. cynocephalus*, even though several small individuals were present. Unfortunately, the lack of *S. m. nullarborensis* material at this stage prevents a more thorough statistical analysis than that conducted for the permanent premolar. However, dimensions of most measurements fall well outside the known range of *S. m. maddocki* supporting its current designation as a separate subspecies.

A probably late Pleistocene age is attributed to the Lindsay Hall Cave deposit, based on the similarity of *S. m. nullarborensis* to *S. m. maddocki*, and the co-occurrence of another widespread, but undescribed sthenurine. The bone-bearing strata of Lindsay Hall Cave may equate with unit 2 in Madura Cave (Lundelius 1963; Lundelius & Turnbull 1989) which has also yielded this undescribed species. Support for this would rely on a detailed stratigraphic investigation of cave deposits in the area.

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THE COOK 007 METEORITE: A NEW H4 CHONDRITE FROM SOUTH AUSTRALIA

*By M. ZBIK**

Summary

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The Cook 007 meteorite, a single stone of over 100 kg in weight, was found at Cook in 1989. It has been classified as an H4 chondrite of shock facies S5-6 and contains olivine ($\text{Fa}_{19.5-03}$ n = 30), orthopyroxene ($\text{Fs}_{17.5-1.2}$ n = 15), clinopyroxene maskelynite, nickel-iron and troilite. Mineral compositions and textures indicate that Cook 007 was a metamorphosed part of the H-meteorite parent body and was very strongly shocked before reaching the Earth.

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Introduction

A single mass of the Cook 007 meteorite weighing over 100 kg, was found at Cook on the South Australian part of the Nullarbor Plain (Fig. 1), in 1989. The approximate co-ordinates of the locality are 30°37'S, 130°25'E. The meteorite was collected illegally and exported to the United States of America. The South Australian Museum obtained a piece from an American meteorite dealer, Mr Allan Lang in April of 1991.

In recent years the Nullarbor Plain has proved to be a productive area for the recovery of meteorites (Bevan

1992; Bevan & Binns 1989a, 1989b) and in the last few years has attracted the attention of illegal meteorite collectors. Under legislation enacted by the Government of South Australia, all meteorites found in the State are the property of the South Australian Museum. An unfortunate consequence of the illegal trade in meteorites is the loss of important information on the exact date and location of the find. In accordance with the guidelines on the nomenclature of meteorites from the South Australian Nullarbor (Bevan & Pring 1993), the meteorite has been named Cook 007, being the seventh meteorite to be recorded from the Cook area.

Physical description

The piece of meteorite obtained from the United States weighs 26.2 kg. It is irregular in shape and is about 35 cm in length, 50 cm in width, 4-11 cm thick and polished on one side. The specimen is currently on display in the meteorite exhibition in the South Australian Museum. The piece has a dark brown 1 mm thick weathering crust covering the outer surface. The interior of the stone shows no sign of weathering, but the heavy weathered crusts covering the surface indicate that the meteorite had been exposed to the elements for many years. A number of quartz grains, probably of aeolian origin, are incorporated into the weathered crust. The interior of the meteorite is black in colour and medium to fine grained. In thin section the meteorite is generally dark coloured (Fig. 2). The chondrules and chondrule fragments are partly recrystallised and well defined boundaries are recognisable even without using crossed polars. They are typically less than 0.5 mm in diameter but some chondrules measure up to 1 cm in diameter. Metal and troilite occur as finely disseminated grains throughout the matrix. A slice was cut and a polished thin section was prepared and used for petrographic examination and electron microprobe analyses.

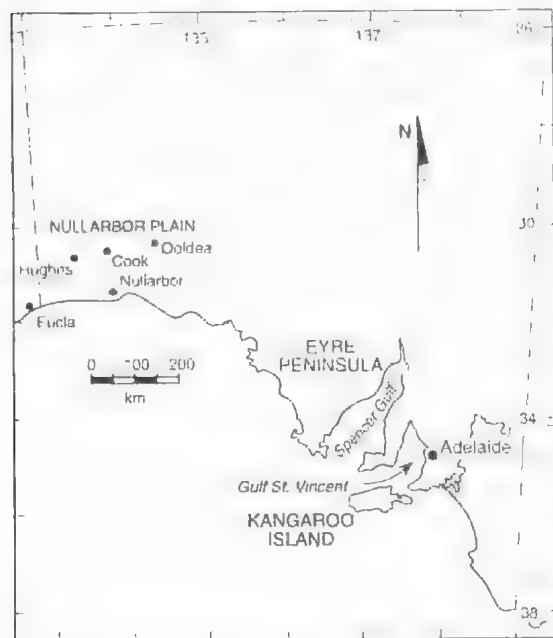


Fig. 1. Map of South Australia showing the approximate location of the Cook 007 meteorite.

* Polish Academy of Sciences, Space Research Centre, Warsaw, Poland

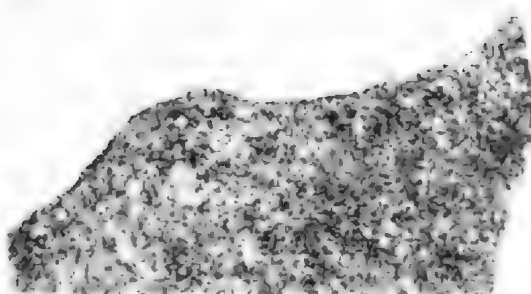


Fig. 2. Photomicrograph of the (thin) section of the Cook 007 meteorite (length of the section 5 cm) showing large dark (staining) area and granular structure full of chondrules and chondrule fragments.

Mineralogy

Compositions of the silicate minerals were determined with a JEOL electron microprobe at the University of Adelaide Centre for Electron Microscopy and Microbeam Analysis. Analyses were made using an accelerating voltage of 15 kV, a sample current of 3 nA, and a beam width of 5 μ m. Mineral analyses are presented in Table 1.

Well-defined chondrules and chondrule fragments are composed predominantly of olivine and orthopyroxene. "Barred" chondrules are composed of olivine or olivine and orthopyroxene and contain thin lamellae of feldspar glass. Fig. 3 shows a fragment of a large barred chondrule which contains bars of olivine and turbid lamellae of glass. The glass has a bytownite composition, and is probably maskelynite. Some large and strongly shocked olivine grains that occur as bright

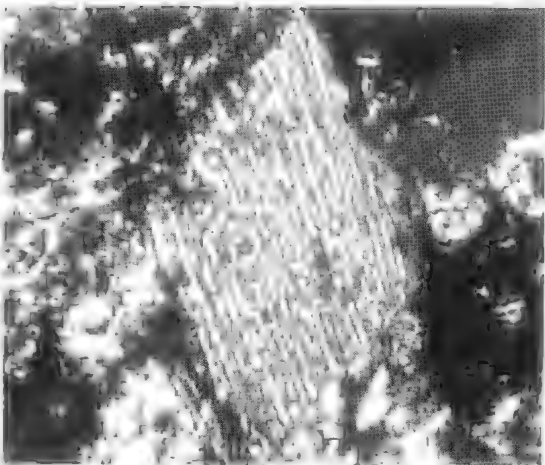


Fig. 3. Photomicrograph of the Cook 007 meteorite in thin section, showing fragment of barred olivine chondrule (about 1 mm in diameter).

purple crystals under crossed nicols are unusual and need further investigation. Chondrules composed of radial pyroxene crystals are also present (Fig. 4). Several of these display a cryptocrystalline structure (Fig. 5) with strong wavy extinction. A number of granular olivine-pyroxene chondrules and porphyritic pyroxene chondrules are present. They contain some coarse, euhedral olivine grains and have a poikilitic texture. These olivine grains contain a network of planar fractures (Fig. 6), which are filled by troilite and metallic Fe, Ni. The occurrence of strong mosaic extinction, solid state recrystallised areas and abundant

TABLE 1. Average chemical compositions of major minerals in the Cook 007 meteorite.

oxide	olivine	orthopyroxene wt%		clinopyroxene	maskelynite
	wt%	core	rim	wt%	wt%
n.....	30	15	15	30	11
SiO ₂	37.8	53.5	53.6	51.3	47.1
TiO ₂	0.1	0.1	0.2	0.7	0.1
Al ₂ O ₃	—	0.3	0.4	1.3	30.7
FeO	18.1	11.7	9.9	5.1	0.6
MnO	0.5	0.5	0.5	0.3	0.1
MgO	41.9	30.2	27.0	18.9	1.6
CaO	0.03	0.5	4.8	17.0	13.2
NaO ₂	—	—	—	0.6	2.8
K ₂ O	—	—	—	—	0
Cr ₂ O ₃	—	0.3	0.6	0.9	—
Total	98.3	97.1	96.7	96.1	96.4
	Fs _{19.5}	Fs _{17.5}	Fs _{15.3}	Fs _{8.4}	Ab _{21.7}
		En _{80.7}	En _{74.4}	En _{55.6}	An _{72.3}
		Wo _{1.0}	Wo _{9.5}	Wo _{36.0}	

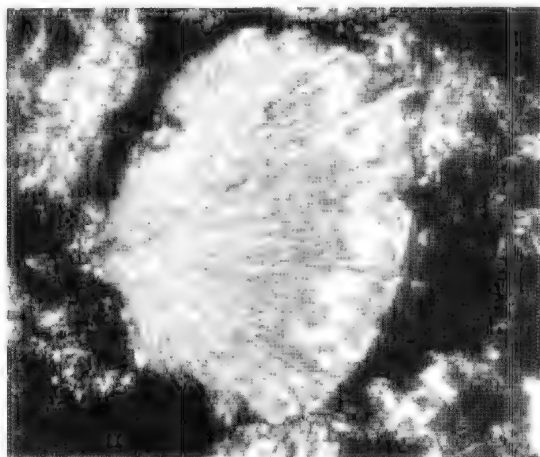


Fig. 4. Photomicrograph of the Cook 007 meteorite in thin section, showing a radial pyroxene chondrule (about 0.5 mm in diameter).

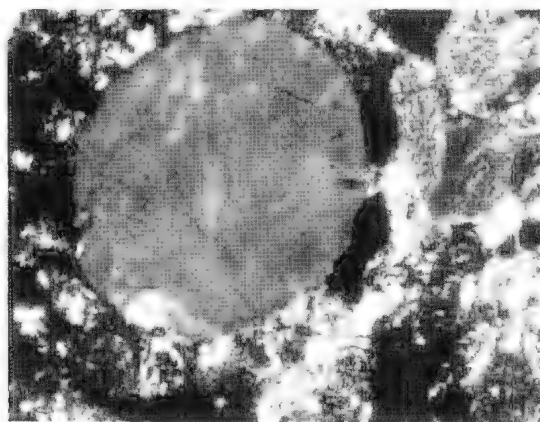


Fig. 5. Photomicrograph of the Cook 007 meteorite in thin section, showing a cryptocrystalline pyroxene chondrule (about 1 mm in diameter).



Fig. 6. Photomicrograph of the Cook 007 meteorite in thin section, showing planar fractures in olivine crystal (about 0.2 mm in diameter).

opaque "mixed" melting which occurs as veins and pockets within the matrix indicates that the meteorite has undergone a high degree of shock metamorphism. Distinct darkening referred to as "shock blackening" (Heymann 1967) is a common feature of this meteorite. Polycrystalline "mixed melt" material surrounds "islands" of unmelted but partly recrystallised crystals. Several porphyritic olivine chondrules display a zoned mineralogy. Euhedral olivine crystals are in contact with low-Ca pyroxenes, with calcium-rich pyroxenes present as thin rims on these and also as fine needles set in the glass of plagioclase composition. The matrix consists of melts, melt pockets and veins, forming a network of complex branches surrounding the unmelted chondrules and chondrite matrix. This indicates in-situ melting of the host material and shows shock blackening. Such a structure has low porosity. The absence of a network of joined intergranular pores protects the interior of the meteorite from being weathered (Zbik 1982). All feldspar present has been changed to maskelynite which is abundant as small turbid patches throughout the matrix. Nickel-iron metal and troilite occur as accessory minerals.

Microprobe analyses show that the olivine in the Cook 007 meteorite is equilibrated with a mean fayalite content of $Fa_{9.5 \pm 0.3}$ $n = 30$. The orthopyroxene shows only a small variation in chemical composition with a mean ferrosilite content of $Fs_{17.5 \pm 1.2}$ $n = 15$ and a wollastonite content of 1 mol%. Some pyroxene phenocrysts contain calcium-rich rims. These rims have a composition of $Fs_{15.3}$ with a wollastonite content of $Wo_{9.5}$ mol%. The composition of the clinopyroxene needles within the glass is $Wo_{36.0}$ $En_{55.6}$ $Fs_{8.4}$ (30 analyses) (Fig. 7). The maskelynite glass has yielded a composition similar to bytownite (11 analyses). The poor quality of microanalyses is a direct result of the high degree of shock metamorphism.

The pyroxene geothermometers of Wells (1977) and Lindsley (1983) suggest that the Cook 007 meteorite was heated to temperatures of between 600°C and 700°C during metamorphism while the meteorite was

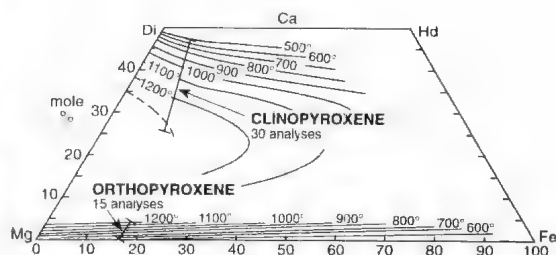


Fig. 7. Silicate mineral chemistry in Cook 007 meteorite. Isotherms show temperature calculations based on the calcium content of orthopyroxenes and clinopyroxenes (Lindsley 1983).

still part of the large H type of the meteorite parent body. After this the meteorite was probably remelted in a major part by impact and heated to a temperature between 1100°C and 1200°C, as indicated by the chemical zoning of pyroxene grains.

Classification

The Cook 007 meteorite has been classified as an H4 chondrite. The olivine composition ($\text{Fe}_{19.5+0.3}$) is within the range of the H chondrites (Keil & Fredriksson 1964). The highly equilibrated mineral compositions, crystalline matrix, and a well defined chondrule boundaries, suggest that Cook 007 belongs to the type 4 classification of Van Schmus & Wood (1967). The wollastonite content of the orthopyroxene is similar to that found in other H4 chondrites (Scott *et al.* 1986). The presence of undulatory extinction, the strong planar fracture formation in olivine, plagioclase

feldspar altered to maskelynite, occurrence of mechanical polysynthetic twinning in orthopyroxene and the degree of crystal fracture all indicate that the meteorite was strongly shocked after metamorphism. The shock facies is estimated to be S5-6; strongly to very strongly shocked according to the classification scheme of Stöffler *et al.* (1991).

Acknowledgments

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A MAJOR RANGE EXTENSION AND NEW ECOLOGICAL DATA ON OXYURANUS MICROLEPIDOTUS (REPTILIA: ELAPIDAE)

BRIEF COMMUNICATION

Summary

The inland Taipan (*Oxyuranus microlepidotus*) is a large elapid snake endemic to Australia. Considering both venom toxicity and average venom yield per bite, *O. microlepidotus* is the world's most dangerous snake¹. Despite its size and medical and scientific significance, the status and distribution of this snake, have been difficult to ascertain. After being described in 1879, *O. microlepidotus* was not found again until 1974². Following its rediscovery, it has been recorded from the channel country of Cooper Creek and Georgina and Diamantina Rivers of south-western Queensland and north-eastern South Australia². *O. microlepidotus* is a rarely seen snake because most of its life is spent in rat burrows³.

BRIEF COMMUNICATION

A MAJOR RANGE EXTENSION AND NEW ECOLOGICAL DATA ON
OXYURANUS MICROLEPIDOTUS (REPTILIA: ELAPIDAE)

The Inland Taipan (*Oxyuranus microlepidotus*) is a large elapid snake endemic to Australia. Considering both venom toxicity and average venom yield per bite, *O. microlepidotus* is the world's most dangerous snake¹. Despite its size and medical and scientific significance, the status and distribution of this snake, have been difficult to ascertain. After being described in 1879, *O. microlepidotus* was not found again until 1974². Following its rediscovery, it has been recorded from the channel country of the Cooper Creek and Georgina and Diamantina Rivers of south-western Queensland and north-eastern South Australia³. *O. microlepidotus* is a rarely seen snake because most of its life is spent in rat burrows⁴.

In April 1992, a large elapid was collected on the Coober Pedy to William Creek Road (29°03'S, 135°03'E) (Fig. 1) by local contractor Jeff Boland. He recognised that the snake was different from the Western Brown (*Pseudonaja nuchalis*) and Mulga Snake (*Pseudechis australis*) with which he was very familiar. Jeff Boland subsequently collected a sloughed skin from the Moon Plain (28°52'S, 134°50'E) (Fig. 1) and sent both the specimen and the slough to the author.

The dorsal scales of the specimen were uniformly dark brown with the head nearly black. The specimen and the slough had 23 mid-body scale rows and a single anal scale. These characteristics enabled the snake and the slough to be confidently identified as *O. microlepidotus*. The scalation of the Coober Pedy specimen closely matched that of *O. microlepidotus* specimens from Moonbha except that rather than the lower primary temporal scale extending to the lip between the 5th and 6th labials, this scale had fused with the 6th labial in the Coober Pedy specimen. Inspection of other specimens in the South Australian Museum indicates that the status of the lower primary temporal scale is considerably plastic in *O. microlepidotus*.

O. microlepidotus can be further distinguished from the sympatric, and highly variable *P. nuchalis* in having a longer head, smaller and more numerous nuchal scales, a pronounced canthus and plain ventral scales as distinct from spotted or dark edged ventral scales in *P. nuchalis*. In addition, most *P. nuchalis* from within the range of the *O. microlepidotus* exhibit irregular black spots or black crossbands, whereas these bands were absent from the Coober Pedy and Moonbha specimens of the *O. microlepidotus*.

In the winter of 1992, two road-killed *O. microlepidotus* were found on the Coober Pedy to Mt Barry Road (28°34'S, 134°54'E, 28°33'S, 134°55'E [SAM R40464]), a live specimen was sighted on the Dingo Fence four kilometres south of the original locality (29°05'S, 135°03'E) and a further specimen was killed at Tom Cat Hill (29°00'S, 134°45'E) in Coober Pedy (Fig. 1). A further road killed specimen was located on the Coober Pedy to Mt Barry Road (28°57'S, 134°47'E [SAM R42484]) in September 1993. South Australian Museum records are denoted by the prefix SAM. On September 6, 1993 a live *O. microlepidotus* was captured by Jeff Boland on the Moon Plain, adjacent to the Breakaways Reserve. The following week a road killed specimen (29°00'S, 135°10'E) was collected approximately 40 km east of Coober Pedy.

The live specimen was captured in the rain with a strong wind blowing and a recorded temperature at Coober Pedy of only 15°C. This snake was uniformly black on the dorsal surface with a white, unmarked ventral surface. One month after its capture the snake sloughed, revealing a yellowish belly and a dark brown dorsal surface with black edges to some scales producing a slight herring-bone pattern. The head remained a glossy black colour following the slough.

The *O. microlepidotus* from Coober Pedy region were about 500 km from the nearest known *O. microlepidotus* locality at Goyder Lagoon, in north-eastern South Australia. The Coober Pedy population of *O. microlepidotus* is separated from that of the channel country by the huge salina of Lake Eyre and the dunefields of the Simpson Desert. The discovery of *O. microlepidotus* near Coober Pedy is highly significant as it represents the first known occurrence of the species near a considerable population centre and also raises the possibility of a much more expanded range than previously recognised for this important snake.

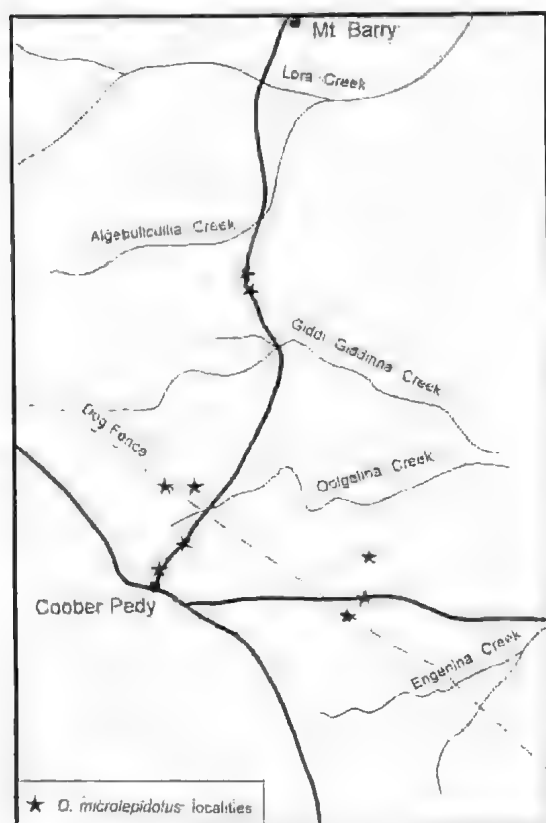


Fig. 1. New records of *Oxyuranus microlepidotus* in the Coober Pedy region.

The Coober Pedy specimens of *O. microlepidotus* were found from April–September. Interestingly, the Goyder Lagoon population of *O. microlepidotus* has been recorded predominantly in March and April^{4,5} whereas Covacevich³ reports that *O. microlepidotus* only emerges for 2–3 weeks in late winter–early spring. Although Covacevich³ indicates that *O. microlepidotus* are predominantly active on still days, Mirtschin⁴ collected several individuals on windy days. The capture of the specimen near the Breakaways Reserve on a cold, wet, windy day indicates that these snakes may be encountered at any time throughout autumn, winter and spring. *O. microlepidotus* are possibly also active in cracks and mammal holes during the warmer months but are not recorded because they do not need to come to the surface to bask.

O. microlepidotus records from the Coober Pedy region were found in two different habitats. Five of the records were from cracking gypseous soils. Four of these records were from a large area of gypseous soils known as the Moon Plain. These soils support little or no perennial vegetation. Cover and species diversity of annual vegetation vary dramatically depending on the season. The dominant, albeit sparse, vegetation during October 1992 consisted of *Atriplex spunglosa*, *Salsola kali*, *Helipterum floribundum*, *Isotriaena leptolepis*, *Arabisella pinnatifida* and the grasses *Emicarpogon polyphyllus*, *Panicum decompositum*, *Aristida amplexicaulis*, *Aristida pectinata*, *Eragrostis setifolia* and *E. dielsii*. Vegetation cover was greatest in the small run-on areas in the undulating plain. These low lying areas were also the most heavily cracked.

Two other records were from gibber country dominated by the Ordovician Saltbush *Atriplex nummularia*. Other common plants included *Sclerolaena intricata*, *Atriplex spunglosa*, *Sarcosium* and *Salsola kali*. Small gilgai depressions within this habitat contained cracking clay and were vegetated with several grass and daisy species.

The plains country around Coober Pedy is very heterogeneous and the two habitats described above often form a mosaic with the gibber more common on high ground and the gypseous soils usually in low lying country. Therefore snakes in this region may depend upon, or prefer, either habitat and yet be recorded crossing between areas of favoured habitat.

The cracking gypseous soil habitat is very similar to the preferred habitat described for *O. microlepidotus* at Clifton Hills, South Australia⁴ and in Queensland⁶ although they have also been recorded from gibber plains and sand dunes⁵. These cracking plains therefore appear to be the key habitat for the *O. microlepidotus*. The cracking gypseous plains are quite widespread near the south-west margin of the Lake Eyre Basin and are often associated with run-off zones from breakaway country. These plains are often inter-connected by creeks which possibly also provide appropriate habitat.

Interestingly the Moon Plain and surrounding gypseous regions were not identified as potential sites for *O. microlepidotus* based on climatic indices⁷. Habitat and biological indices, rather than climatic variables may therefore be more important than climate in determining the range of *O. microlepidotus*.

The eastern population of *O. microlepidotus* feeds extensively on the Long-haired Rat (*Rattus villosissimus*) with which its ecology and distribution have been inextricably linked⁴. The evolution of a large size, a rapid snap-release bite and extremely potent venom in *O. microlepidotus* is

believed to be a response to their predation on mammals which can defend themselves by biting savagely¹. Therefore, particular emphasis was placed on searching for *R. villosissimus* or other similar sized mammals in the Coober Pedy region, to predict the potential range of *O. microlepidotus*.

Field surveys were conducted during 1992–1993 in cracking clay regions adjacent to the *O. microlepidotus* records on Mt Barry, Anna Creek, Hilla Kalioa and Stuart Creek Stations to ascertain whether *O. microlepidotus*, or their prey species, occupied a more extensive range. The striking feature of the cracked gypseous soil localities was the diversity of mammals and paucity of reptiles. Of particular note was the presence of Plains Rats (*Pseudomys australis*). Although *R. villosissimus* reached the Coober Pedy region in 1973–74 (J. Boland, K. Greenfield pers. comm.) they do not appear to inhabit the region normally and were not recorded in this survey. *P. australis*, Forrest's mice (*Lagadina forresti*), Desert Mice (*Pseudomys desertor*), House Mice (*Mus domesticus*), Pouched Plungales (*Plomigale gilesii*) and Dunnarts (*Sminthopsis macroura*, *S. crassicaudata*) were located over a wide range. Mammal densities were higher in the cracking gypseous soils than in other habitats in the region⁸. While the adult *O. microlepidotus* probably feed predominantly on *P. australis*, *L. forresti* and the occasional band, juvenile snakes could feed on *P. gilesii* and *M. domesticus*.

Because eight confirmed records now exist from different localities, initial suspicions that the specimens represented snakes that were artificially translocated from their original range can probably be discounted. However, it is not known whether this apparent range expansion is a recent phenomenon, facilitated by mobility of the north-eastern population, or whether *O. microlepidotus* have occupied the plains around Coober Pedy for a long period. Considering the dependence on the *R. villosissimus* in the channel country, a potential scenario is that the *O. microlepidotus* followed the rats from north-eastern South Australia through to Coober Pedy during the rat plague of 1916. It is unlikely, however, that *O. microlepidotus* could have expanded its range by over 400 km during the course of a single rat plague. A more feasible explanation is that *O. microlepidotus* have always inhabited the gypseous plains around the south-western margin of the Lake Eyre basin but the sparseness of the human population combined with the predominantly underground habit of the snake have accounted for the paucity of records. These same factors probably explain why *O. microlepidotus* eluded discovery in the Birdsville region for so long. Increased snake numbers as a result of large mammal populations which have responded to good seasons, combined with increased vigilance and awareness of local residents probably explain why the *O. microlepidotus* was discovered in the region in 1992. A continued interest in this species is predicted to result in the discovery of *O. microlepidotus* over a broader range in cracky gypseous country to the south and west of Lake Eyre.

This paper is dedicated to Jeff Boland whose interest and awareness resulted in the discovery of *O. microlepidotus* near Coober Pedy. Thanks also go to Mick and Ben Evans, Greg Stagbourn, Peter Paisley, Bec Mussared, Katherine Moseby, Steve and Tania Green, John Fewster and Zoe Bowen for assistance with field work and to Mark Hutchinson, Jeanette Covacevich and Peter Mirtschin for help in the preparation of this paper. Frank Badman assisted with plant identification.

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**GROWTH IN THE AUSTRALIAN BURROWING FROG,
CYCLORANA AUSTRALIS (GRAY)
(ANURA: LEPTODACTYLIDAE)**

BRIEF COMMUNICATION

Summary

The majority of known Australian fossil frogs have been identified by the characteristics of the ilium, a distinctive bone in which the morphology varies greatly between family, genus, and species¹⁻³. Hence it is now used extensively as a diagnostic tool¹⁻³.

The physical characteristics of the frog can be identified from the size and points for muscular attachment on the ilium. These features represent adaptations to the environment. For example a short ilial shaft is characteristic of a burrowing frog which does not make long jumps^{1,2,4}.

BRIEF COMMUNICATION

GROWTH IN THE AUSTRALIAN BURROWING FROG, *CYCLORANA AUSTRALIS* (GRAY)
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The majority of known Australian fossil frogs have been identified by the characteristics of the ilium, a distinctive bone in which the morphology varies greatly between family, genus, and species^{1,3}. Hence it is now used extensively as a diagnostic tool^{1,3}.

The physical characteristics of the frog can be identified from the size and points for muscular attachment on the ilium. These features represent adaptations to the environment. For example a short ilial shaft is characteristic of a burrowing frog which does not make long jumps^{2,4}.

To permit extrapolation of the size of a frog from the length of the ilium requires an understanding of the relationship between the ilium length (IL) and snout to vent length (S-V).

It is generally considered that the ilium grows linearly in relation to the S-V of the donor animal³.

However, the data from which these assumptions are made have been based on small sample sizes, and little is known of early ontogenetic changes^{1,3,5}. It is also important to note that it is common in the Animal Kingdom for a change in size to result in a change of the proportions of the body. A simple example of such allometric growth can be seen during the development of human beings, in which a large change in the proportions of the limbs and the head, in relation to trunk size, can be seen when children are compared with adults⁶.

This study was an attempt to determine the nature of growth, from juvenile to adult form, of the burrowing frog *Cyclorana australis* (Gray, 1842) via the relationship between ilial length and snout-vent length.

The ilia examined were dissected from 24 preserved specimens in the collections held at the Department of Zoology, University of Adelaide. Before dissection the S-V of each specimen was measured with a pair of NSK electronic digital callipers. The pelvis was then removed, and soaked in bleach to loosen muscle, before being transferred to a 37°C oven to dehydrate for 24 hours. The IL for each ilium was measured using electronic digital callipers, with the aid of

a Wild M3 dissecting microscope. Iliac length was expressed as the distance between the tip of the dorsal acetabular expansion, and the end of the ilial shaft¹.

The characteristics of the ilium of the specimens examined did not differ significantly from those described¹ (see Fig. 1). The S-V ranged 20.0 mm to 83.1 mm, and IL 6.1 mm to 32.0 mm.

A linear regression comparing IL with S-V showed a direct relationship between the body length and the length of the ilium, i.e. the ilium grows linearly in relation to the body length throughout ontogeny (see Fig. 2).

The linear growth of *C. australis* permits a very accurate method for estimating the size of an individual from a disarticulated ilium.

I am greatly indebted to Prof. M. J. Tyler for the opportunity to undertake this research and for constructive criticism of the early drafts, and I am extremely grateful for the assistance from K. Maurice-Jones in the production of the figures.

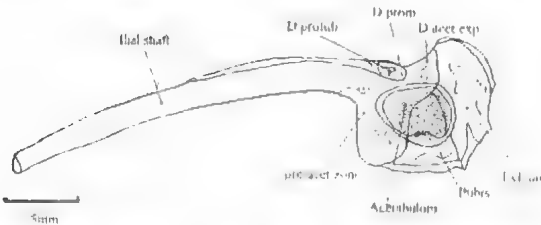


Fig. 1. Left lateral aspect of *Cyclorana australis* pelvic girdle (IL = 30.6 mm, S-V = 82.1 mm).
Abbreviations: D. acet. exp. = dorsal acetabular expansion; D. prom. = dorsal prominence; D. protub. = dorsal protuberance; pre-acet. zone = pre-acetabular zone.

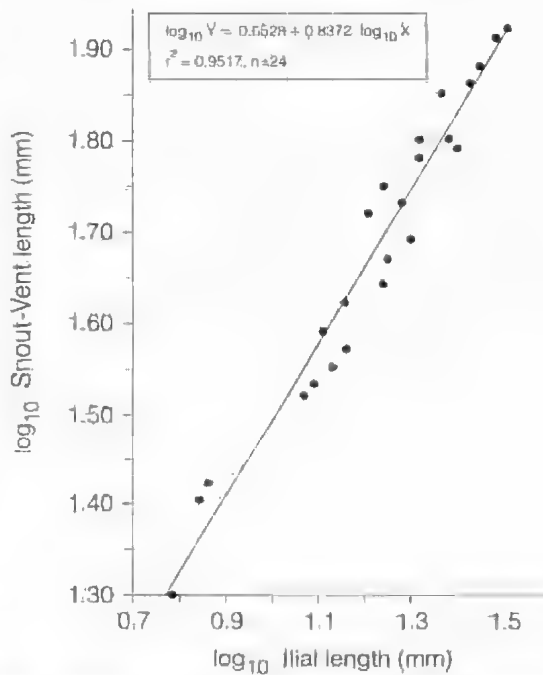


Fig. 2. Regression line of ilium length of *Cyclorana australis* with snout-vent length. For $x = 18.30$ mm, $y = 51.25$ mm (95% confidence limits = 49.36 – 53.23).

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TRANSACTIONS OF THE

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VOL. 118, PART 3

**MORPHOLOGY AND REPRODUCTIVE BIOLOGY OF
LIMNODYNASTES SALMINI, L. CONVEXIUSCULUS AND
MEGISTOLOTTIS LIGNARIUS
(ANURA: LEPTODACTYLIDAE: LIMNODYNASTINAE)**

BY MARGARET DAVIES & GRAEME F. WATSON†*

Summary

Davies, M. & Watson, G. F. (1994) Morphology and reproductive biology of *Limnodynastes salmini*, *L. convexiusculus* and *Megistolotis lignarius* (Anura: Leptodactylidae: Limnodynastinae). *Trans. R. Soc. S. Aust.* 118(3), 149-169, 30 November, 1994.

External morphology, osteology, structure of the larval chondrocranium, development and call characteristics of the limnodynastine frogs *Limnodynastes salmini* and *L. convexiusculus* are described and compared with similar data derived from *Megistolotis lignarius*. These data are presented to contribute to our understanding of the biology of the anuran fauna as well as to a wider analysis of the genera *Limnodynastes* and *Megistolotis* being undertaken to examine the hypothesis that *M. lignarius* is the sister taxon to *L. convexiusculus* and that *L. salmini* is the closest relative to this species pair.

Key Words: *Limnodynastes convexiusculus*, *Limnodynastes salmini*, *Megistolotis lignarius*, frogs, calls, larvae, life history, osteology, morphology, larval chondrocrania.

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Summary

DAVIES, M. & WATSON, G. F. (1994) Morphology and reproductive biology of *Limnodynastes salmini*, *L. convexiusculus* and *Megistolotis lignarius* (Anura, Leptodactylidae, Limnodynastinae). *Trans. R. Soc. S. Aust.* 118(3), 149-169, 30 November, 1994.

External morphology, osteology, structure of the larval chondrocranium, development and call characteristics of the limnodynastine frogs *Limnodynastes salmini* and *L. convexiusculus* are described and compared with similar data derived from *Megistolotis lignarius*. These data are presented to contribute to our understanding of the biology of the anuran fauna as well as to a wider analysis of the genera *Limnodynastes* and *Megistolotis* being undertaken to examine the hypothesis that *M. lignarius* is the sister taxon to *L. convexiusculus* and that *L. salmini* is the closest relative to this species pair.

KEY WORDS: *Limnodynastes convexiusculus*, *Limnodynastes salmini*, *Megistolotis lignarius*, frogs, calls, larvae, life history, osteology, morphology, larval chondrocrania

Introduction

Limnodynastes Fitzinger comprises 13 species (Tyler 1992), generally accepted to fall into three species groups — the *L. tasmaniensis* group, the *L. dorsalis* group and the *L. ornatus* group (Tyler *et al.* 1979; Roberts & Maxson 1986; Mahony & Robinson 1986).

The composition of these three groups and the complement of the genus has been challenged by Hutchinson & Maxson (1987) who proposed, on the basis of data derived from comparisons of albumin using the immunological technique of micro-complement fixation, that *Limnodynastes* is paraphyletic and that *Megistolotis lignarius* is the closest relative of *L. convexiusculus*. *Limnodynastes salmini* is proposed as the closest relative of these two species, all three falling in the *L. tasmaniensis* species group.

This contention has not been widely accepted (Cogger 1992; Tyler 1992; Littlejohn *et al.* 1993; Roberts & Watson 1993) and the question will not be resolved until data are provided for a broader analysis of the genus. Such data should include morphology, osteology and biological data such as calls and developmental information. Although the recognition of these three taxa is not in dispute, availability of these data varies between them.

Parker (1940) provided morphological descriptions of most species of *Limnodynastes* and included some information on the osteology of the carpalia as well as the nature of the hyoid. In many cases he had limited material available to him. Moore (1961) provided some further morphological data for selected species together with distributional data whilst Lynch (1971) diagnosed the genus on the basis of osteological characters derived from four species, not the taxa under consideration here. *Megistolotis lignarius* was not available, of course, to any of these workers. That genus and species were described very comprehensively by Tyler *et al.* (1979). However, the description did not include a formal description of the skull or of post-cranial elements, although the skull was illustrated. None of these authors examined the chondrocrania of larval forms of the taxa.

As part of a wider study examining the phylogenetic relationships of *Limnodynastes* and *Megistolotis* and of ongoing studies of the biology of Australopapuan frogs, we provide data on the morphology (including data from the chondrocranium) and biology of *L. convexiusculus*, *L. salmini* and *M. lignarius* and consider these data in the light of published literature. Although Parker (1940) provided relatively comprehensive descriptions of the external morphology of *L. salmini* and *L. convexiusculus*, his sample size was necessarily small, so we provide further descriptions including measurements in a standard format to allow for direct comparison between taxa. For the same reason, we include a further illustration of the skull of *M. lignarius* in a composite figure of the skulls of all taxa.

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Materials and Methods

Material cited here is lodged in the collection of the Dept of Zoology University of Adelaide (UAZ), South Australian Museum, Adelaide (SAM), Queensland Museum, Brisbane (QM), Australian Museum, Sydney (AM), and Queensland National Parks and Wildlife Service (Dept of Environment and Heritage), Townsville (QNPWS).

Measurements of adult specimens were recorded to the nearest 0.05 mm by means of dial calipers. The following data were obtained according the method of Tyler *et al.* (1979): snout-vent length (S-V), head length (HL), head width (HW), eye to naris distance (E-N), internarial span (IN), eye diameter (E), tympanum diameter (T).

Initially embryos were reared under fluctuating field conditions; on return to the laboratory, they were reared at $30^{\circ}\pm 1^{\circ}\text{C}$ in glass aquaria ($25 \times 25 \times 8$ cm) containing aerated dechlorinated tap water. Larvae were fed boiled, organically-grown mignonette-lettuce leaves supplemented with Sera Bioflakes pond fish food. Samples of embryos and larvae were preserved in Tyler's (1962) fixative. Measurements of developmental stages were made with dial calipers reading to 0.05 mm or a stereoscopic microscope and ocular micrometer.

The developmental staging system used is that of Gosner (1960). Descriptions of chondrocrania follow the nomenclature of Sokol (1981).

Osteological preparations were made after the methods of Davis & Gore (1947) (single stained) and Dingerkus & Uhler (1977) (double stained).

Illustrations were made using a Wild M8 stereo-dissecting microscope and camera lucida.

Calls were recorded in the field using either a Uher 4000 (*L. salmini*) or a Tandberg S11 (*L. convexiusculus* and *M. lignarius*) portable tape recorder and Beyer M-69 dynamic microphone, at a tape speed of 19 cm/s. The effective temperature of each recorded frog (either water temperature or wet-bulb air temperature depending on where the male was calling) was measured at the calling site. All recordings were analysed on a DSP 5500 digital Sona-Graph (Kay Elemetrics Corp.) using the in-built set-up #10, with playback on a Revox B 7711 reel to reel tape recorder. For each call, two attributes were determined: (i) duration as the interval from the beginning to the end of the note; (ii) dominant frequency (Hz) as the maximum value of the spectrum of power between the cursors for the whole note. Levels of resolution were less than 1 ms for temporal aspects, and less than 40 Hz for dominant frequency. Three calls of each individual were analysed. Calls of *M. lignarius* are those of the holotype and paratype described by Tyler *et al.* (1979) and reanalysed here using more modern

equipment to facilitate comparisons between the three species.

Limnodynastes salmini Steindachner, 1867

FIGS 1-14

Limnodynastes salmini Steindachner, F. (1867) Amphibien in "Reise der österreichischen Frigate Novara von die Erde in den Jahren 1857, 1858, 1859". Zoologie 1(4), 1-70. (State Printer, Vienna).

Type

NHMW 14849 (two syntypes) from Cape York Qld (as Australia) (Cogger *et al.* 1983).

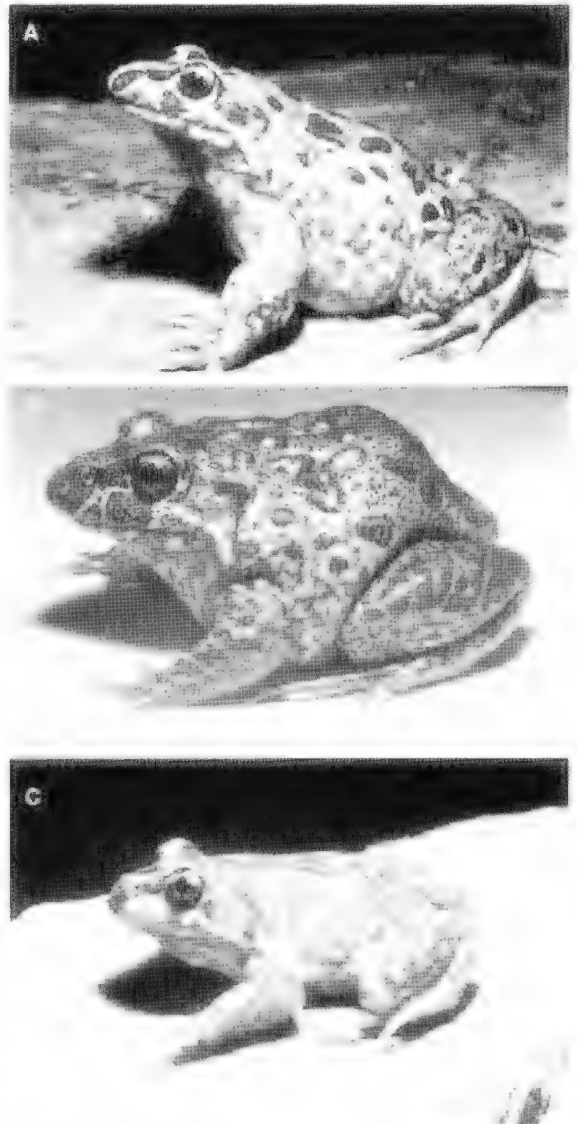


Fig. 1. A. *Limnodynastes salmini*, B. *L. convexiusculus* and C. *Megistolotis lignarius* in life.

Definition

A large species (males 43-76 mm, females 61 mm) characterised by yellowish dorsolateral skin folds, a relatively distinct tympanum, glandular nuptial excrescences in the male, poorly flanged fingers in the female, first finger longer than the second, male call a resonant "unk", deposition of eggs in a foam nest.

Description (based on SAM R 41969)

Head depressed; slightly longer than broad (HL/HW 1.07), slightly more than $\frac{1}{4}$ of snout-vent length (HL/S-V 0.35). Snout prominent, ovoid when viewed from above and rounded in profile (Fig. 1). Nares dorsal in position, their distance from end of snout less than that from eye. Eye to naris distance less than internarial span (E-N/IN 0.92). Canthus rostralis well defined and straight. Loreal region straight, sloping ventrolaterally. Eye moderate in diameter. Tympanum distinct, 0.6 of eye diameter (Fig. 1). Vomerine teeth in long horizontal rows, meeting in midline, posterior to small lateral choanae, but not contacting them. Tongue broad. Vocal sac slits lateral to tongue.

Fingers cylindrical, unfringed, basally webbed (Figs 2, 3); subarticular and palmar tubercles well developed. Supernumerary tubercles at junction of first and second fingers and second and third fingers. Inner palmar tubercles large, outer divided. Nuptial excrescences not detectable. Fingers in order of length $3 > 1 > 2 = 4$.

Hind legs moderately short (TL/S-V 0.40). Toes long, cylindrical with narrow lateral fringes and basal webbing (except between toes 4 and 5) (Fig. 3). Subarticular tubercles large, conical. Large prominent inner metatarsal tubercle; rounded thickening of skin,

but no outer metatarsal tubercle. Toes in order of length $4 > 3 > 5 > 2 > 1$.

Dorsum with well-developed, elevated, pigmented glands. Supralabial glands elongate and prominent (Fig. 1). Skin not covered by spines. Ventral skin smooth, pigmented. Canthal stripe through eye and tympanum to axilla. Two pale (cream) stripes laterally from scapula to groin. Well-defined black spots on dorsum along each side of stripes and medial to them. Groin and back of thighs dark chocolate with white spots.

Variation

The second finger and the thumb on their medial sides are fringed in females (Fig. 2) and nuptial excrescences are glandular in males. The species varies little in its external morphology. The tympanum is more indistinct in some specimens. Hind legs are uniformly moderately short (TL/S-V mean = 0.405, range 0.38-0.42). The head is as long or longer than it is wide (HL/HW, mean = 1.09, range 1.00-1.18). Head length is about $\frac{1}{4}$ snout-vent length (HL/S-V, mean = 0.36, range 0.31-0.39). In all but one case, eye to naris distance was less than internarial span (E-N/IN, mean = 0.87, range 0.70-1.07).

Material examined

Qld: QNPWS N17095, Bundaberg, nr Mon Repos, N28209, N28228, N28251, Lake Nugga Nugga, A851, Gladstone, A6, Southwood N.P. (nr Moonie). SAM R41969-70, UAZ B1730, A1729, B1726 nr Ban Ban Springs.

Osteology (based on AUZ A161) (Fig. 4).

Skull moderately well ossified. Sphenethmoid poorly ossified, not in bony contact with nasals, extending



Fig. 2. Palmar view of the hand of A. female *Limnodynastes convexusculus* (SAM R41983). B. female *L. salmii* (SAM R41969) and C. female *Megistolotis lignarius* (SAM R41986). Scale bar = 5 mm.

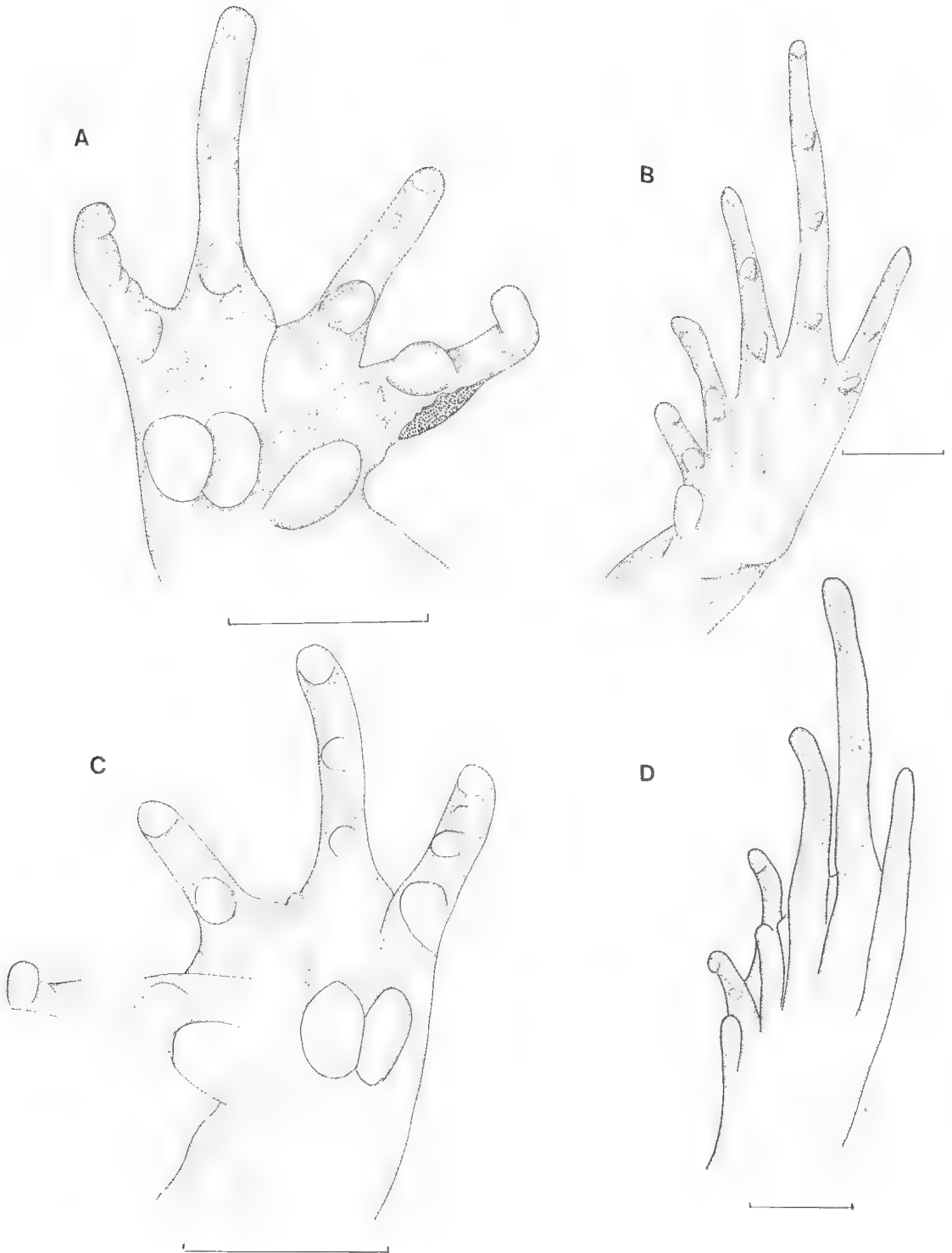


Fig. 3. Palmar view of hand and plantar view of foot of A. *Limodynastes convexiusculus* (SAM R41983) and B. *L. salmini* (SAM R41969). Scale bars = 5 mm.

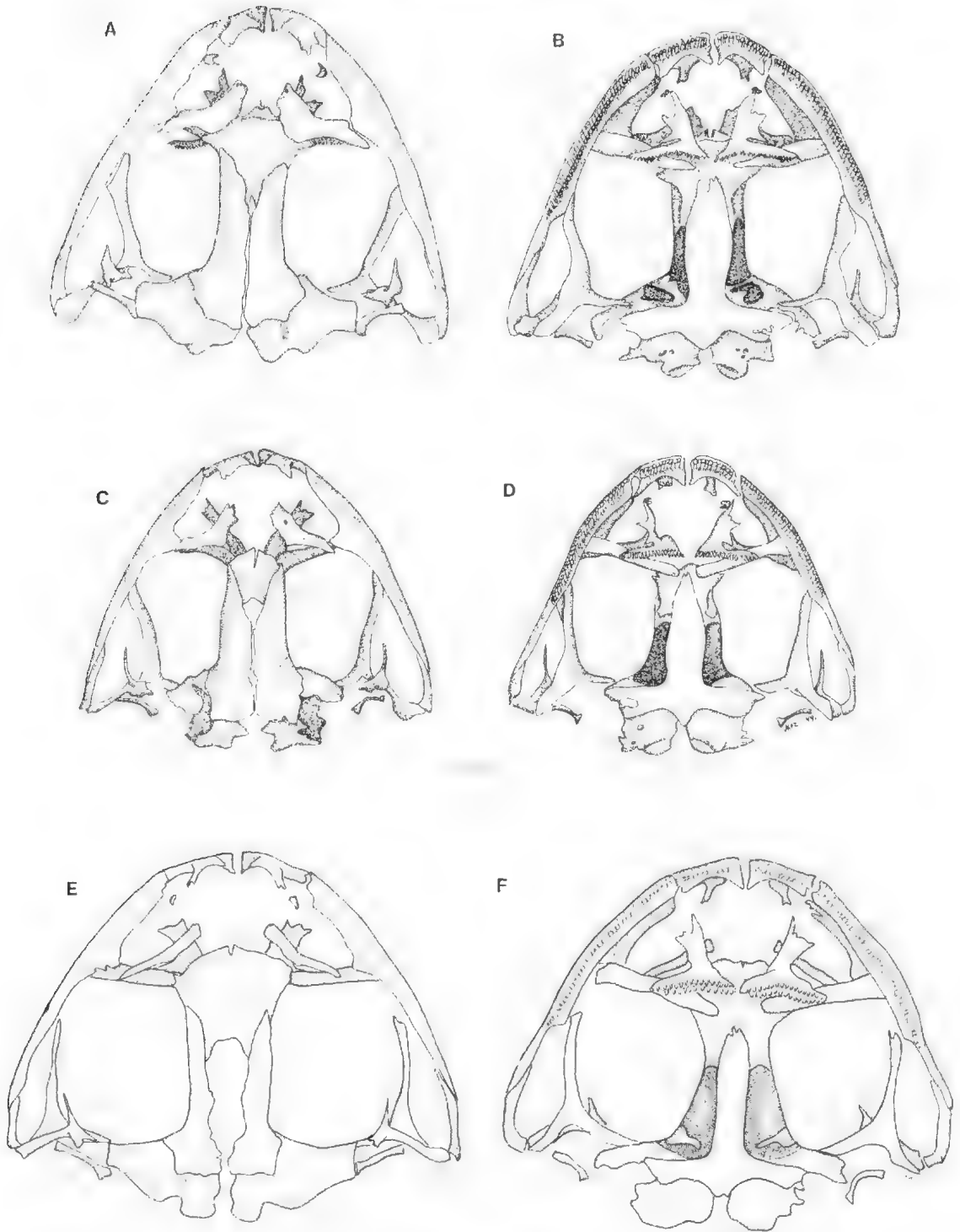


Fig. 4. A. Dorsal and B. ventral views of the skull of *Limnodynastes convexiusculus* (UAZ A 233); C. Dorsal and D. ventral view of the skull of *L. salmini* (UAZ A161); E. dorsal and F. ventral views of the skull of *Megistotis lignarius* (UAZ A1742). Scale bar = 5 mm.

$\frac{1}{3}$ length of orbit in ventral view. Prootic and exoccipital not fused. Exoccipital not ossified dorso- or ventro-medially. Crista parotica short and stocky, not articulating laterally with short expanded otic ramus of squamosal. Frontoparietal fontanelle poorly exposed. Frontoparietals well ossified; anterior extremities extending $\frac{3}{4}$ length of orbit. Orbital edges of frontoparietals straight, not angled posterolaterally. Anterior margin of frontoparietal fontanelle formed by sphenethmoid at a level about $\frac{1}{3}$ anteriorly along length of orbit. Posterior margin undefined because of juxtaposition of frontoparietals medially and lack of medial ossification of exoccipitals. Nasals poorly ossified, maxillary process elongate and moderately broad, in contact with well-developed preorbital process of pars facialis of maxilla. Palatines broad, expanded laterally, running under dentigerous processes of vomer to overlie edges of ventral sphenethmoid medially. Parasphenoid robust. Cultriform process elongate, broad almost reaching medial extremities of palatines. Alae broad, moderately long, expanded laterally, at right angles to cultriform process.

Pterygoid robust. Anterior ramus in short contact with poorly developed pterygoid process of palatal shelf of maxilla. Medial ramus slender overlying alae of parasphenoid. Posterior ramus very robust and elongate. Junction of three rami very robust.

Quadratojugal robust and entire. Squamosal robust with moderately long zygomatic ramus and short expanded otic ramus. Maxilla and premaxilla dentate.

Pars facialis of maxilla deep with well-developed preorbital process.

Alary processes of premaxilla broad, slightly bifurcated dorsally, directed posteriorly. Pterygoid processes of palatal shelf poorly developed. Vomers reduced medially with extremely elongate horizontal dentigerous processes. Columella bony, sigmoid in shape.

Pectoral girdle arciferal and robust. Slender omosternum, broad xiphisternum. Sternum cartilaginous. Clavicles slender, closely applied medially. Coracoids very robust, widely separated medially. Bicapitate scapula robust. Suprascapula about $\frac{1}{2}$ ossified. Anteroproximal crest of humerus moderately well developed.

Carpus of five elements (Fig. 5). Lateral process on medial surface of first metacarpal. Sesamoids absent at junctions of metacarpals and/or phalanges.

Seven procœlous non-imbricate presacral vertebrae. Vertebrae I and II fused. Relative width of transverse processes:

$$\text{III} > \text{IV} > \text{II} = \text{SD} > \text{V} > \text{VI} > \text{VII} > \text{VIII}$$

Sacral diapophyses poorly expanded. Iliia extending very slightly anteriorly to sacral diapophyses. Urostyle crest approx. $\frac{3}{4}$ length of urostyle.

No ilial crest. Dorsal prominence prominent (Fig. 6). Dorsal protuberance ovoid and lateral. Pubis calcified. Three tarsal elements in foot. Prehallux large, hastate, cartilaginous dorsally with bony base.

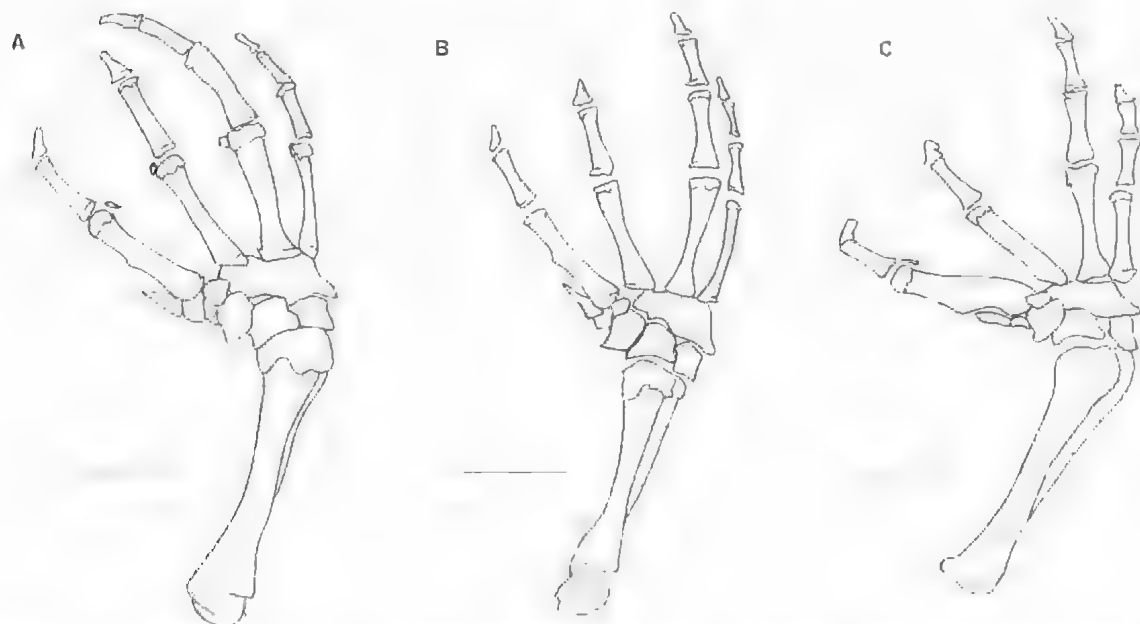


Fig. 5. Dorsal view of the carpus of A. *Limnodonastes convexusculus*, B. *L. salmini* and C. *Megistolotis lignarius*. Scale bars = 5 mm

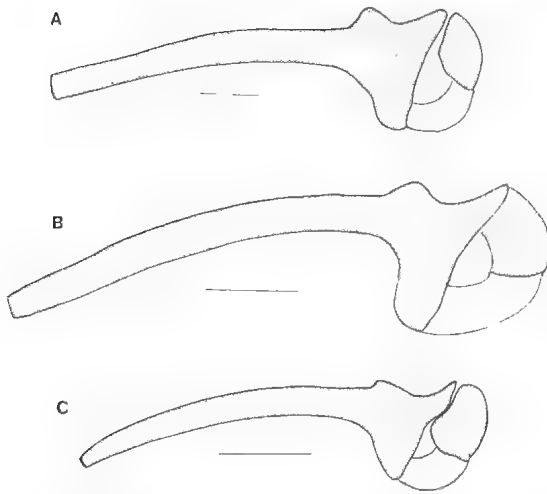


Fig. 6. Lateral views of the ilia of A. *Limnodynastes salmini*, B. *L. convexisculus* and C. *Megistolotis lignarius*. Scale bars = 5 mm.

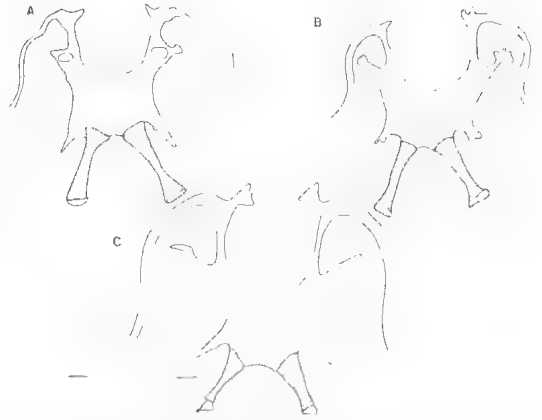


Fig. 7. Ventral views of the hyoid in A. *Limnodynastes salmini*, B. *L. convexisculus* and C. *Megistolotis lignarius*. Scale bars = 5 mm.

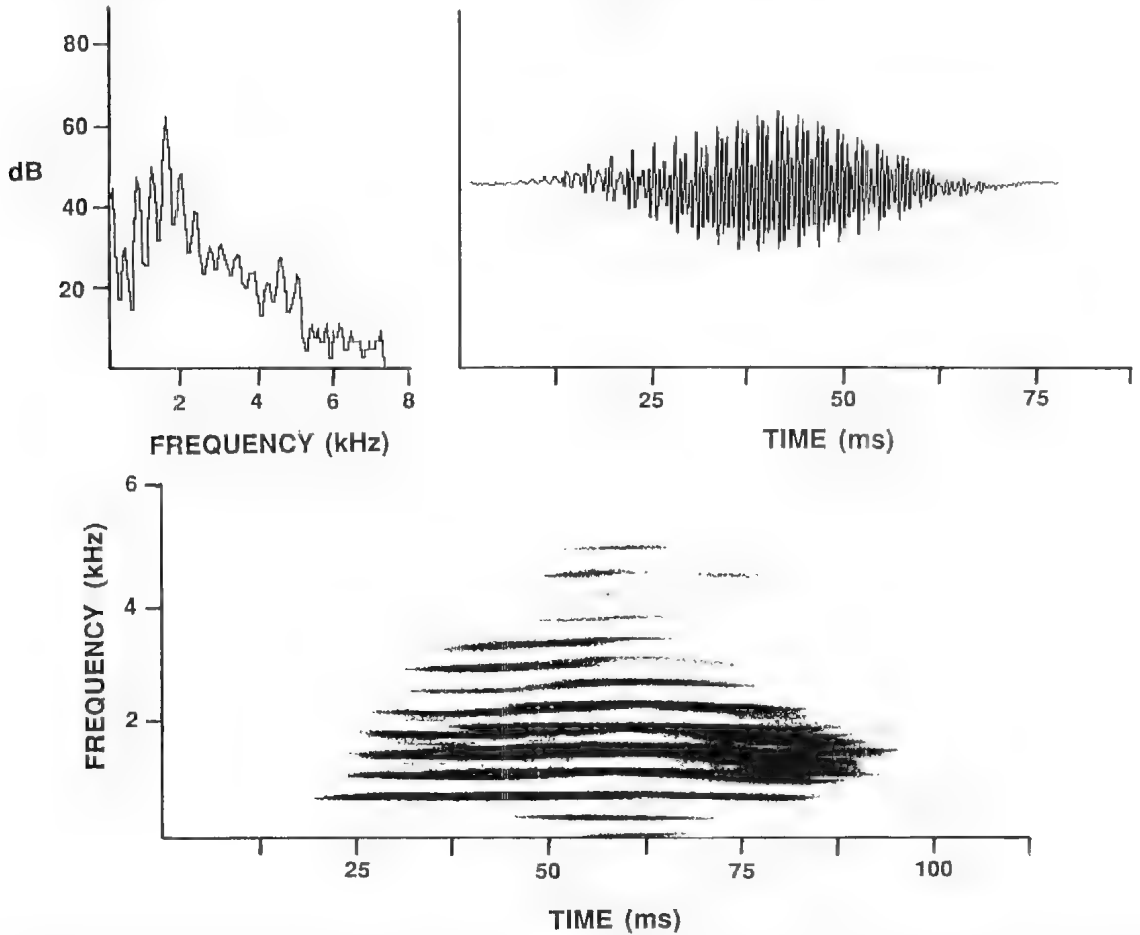


Fig. 8. Power spectrum, waveform and sonagram (sampling frequency 59 Hz) of the advertisement call of *Limnodynastes salmini*. Note that the ordinate for the waveform display is not labelled because it depicts a relative linear scale in volts.

Hyoid plate wider than long; posterior processes slender, asymmetrical in length. Anterior processes short, blunt perforated. Short, broadly based anteromedial processes on anterior hyale. Posterior cornua ossified (Fig. 7).

Variation

Variation in ossification is restricted to the sphenethmoid, nasals and crista parotica. Maximum ossification of the sphenethmoid occurs when the bone extends between the nasals to a point almost midway between them. The condition in Fig. 4 is the minimal condition. However, such ossification does not appear to be size related.

The posteromedial processes of the nasals can show greater development than illustrated while the maxillary process is slightly separated from the preorbital process of the pars facialis of the maxilla in the very large female UAZ A1729.

In two of the specimens examined, the exoccipital and prootic are confluent dorsally, but not ventrally.

but again such ossification does not appear to be size related.

The other features of the cranium do not appear to be variable.

Material examined

UAZ A1729, female, Ban Ban Springs, B1730, male, same locality, B1726, male, same locality, A161, sex not known, Brisbane, B1736, Stage 33 larvae, B 1737, Stage 35 larvae, QNPWS 17095, ?male, Mon Repos nr Bundaberg.

Habitat

Limnodynastes salmini calls from flooded tall grassland, culverts and swamps. Frogs are found beneath dense vegetation and are difficult to locate. Cogger (1992) records that the species burrows. Structure of the metatarsal tubercle indicates this to be a possibility, but we have no direct evidence of this habit.

Advertisement call

The advertisement call of *L. salmini* is a well-tuned, single note (mean duration 67.4 ms, Table 1) repeated regularly in long calling sequences. Call repetition rate

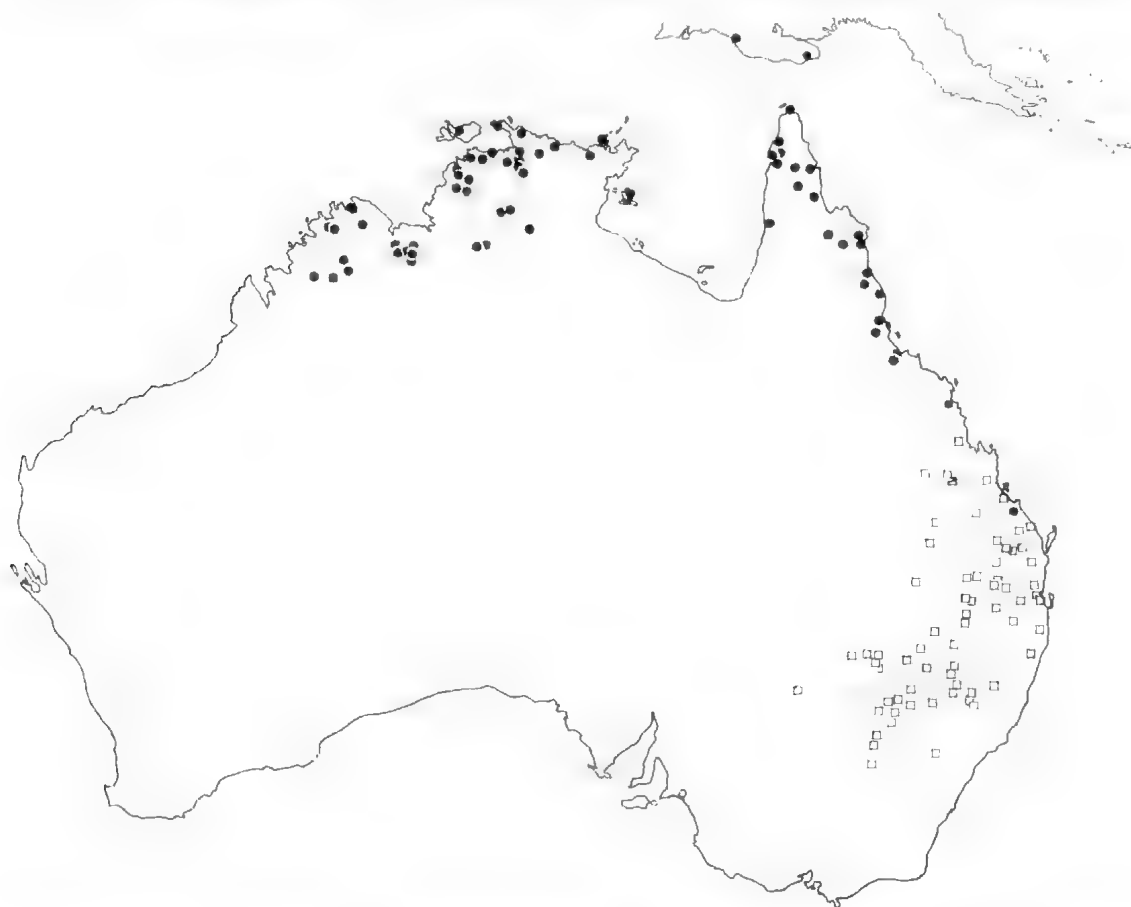


Fig. 9. Distribution of *Limnodynastes salmini* (open squares) and *L. convexiculus* closed circles. Symbols may represent more than one close locality.

TABLE 1. Durations (ms) of the calls of *Limnodynastes salmini*, *L. convexiusculus* and *Megistolotis lignarius*. Means and ranges (shown in parentheses) based on analysis of three calls from each individual listed

Species	No. recorded	Call duration
<i>Limnodynastes salmini</i>	3	67.4 (50-83.2)
<i>Limnodynastes convexiusculus</i>	6	74.7 (67.6-85.6)
<i>Megistolotis lignarius</i>	2	26.6 (21.5-32.4)

for the three individuals reported here was approximately 0.91 calls/s (at an effective temperature of 25.2°C). Waveform and spectrographic displays of a single note and a power spectrum are shown in Fig. 8.

Distribution

Limnodynastes salmini has an eastern Australian distribution, the most northerly record being St. Lawrence (Moore 1961). The most southerly record is near West Wyalong, N.S.W. (Fig. 9). These records cast doubt upon the interpretation of Cogger *et al.* (1983) that the type locality is on Cape York Peninsula.

Natural history

The species is predatory on other species of frogs. One was collected with a *L. ornatus* head first down its throat in the process of being swallowed.

Life history

Eggs are laid in a large, foamy egg mass. Two such spawn clumps contained approximately 1630 and 2430 eggs respectively. These clumps were collected soon after deposition at 1120 on 21.i.1991 near Ban Ban Springs, SE Qld. A sample of ten eggs had a mean capsular diameter of 1.55 mm (range 1.44-1.68 mm) and a mean egg diameter of 1.27 mm (range 1.18-1.34 mm). There were two jelly layers surrounding pigmented eggs which hatched at stage 19 about 24 h after collection (Fig. 10).

Just prior to hatching (still at stage 19), the stomodaeum was a pit anteriorly and a pair of well-developed pigmented adhesive glands projected ventrally. Two pairs of external gills were apparent, the first with two and the second with six short, broad filaments.

At hatching, a depression in the presumptive eye region was apparent.

At 0850 on 24.i.1991, embryos were at stage 21 but the external gills had disappeared. The cornea was

transparent. The mouth had perforated and keratinization had commenced upon the upper beak. The adhesive organs remained extremely prominent, elevated and slightly pigmented (Fig. 10). The nares were perforated, as was the anus as a median aperture.

Twenty-four hours later on 25.i.1991 embryos were at stage 24. The operculum was not fully formed. The horny beak was keratinized and some of the tooth rows were partially detectable. All of these had keratinized by stage 26.

Stage 27 was reached by 27.i.1991, six days after hatching. The spiracle was fully formed. The beak was keratinized as were two upper and three lower labial tooth rows. The labial papillae were fully formed at this stage. Larvae were at stage 29 on 31.i.1991. Stage 35 was reached on 2.ii.1991.

A larva at stage 34 is illustrated in Fig. 11. The body is ovoid and widest at the level of the eyes. The snout is evenly rounded in dorsal view and slightly truncated

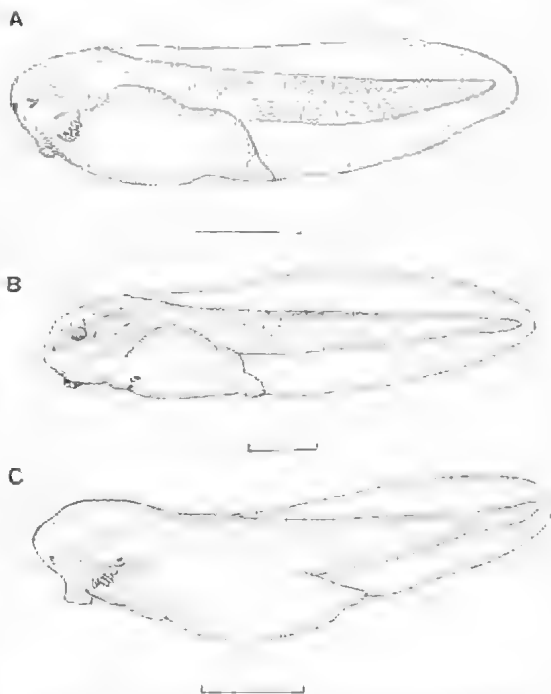


Fig. 10. A, Embryo of *Limnodynastes salmini* at stage 20, B, at stage 21 and C, at stage 19. Scale bars = 1 mm.



Fig. 11. A, Lateral and B, dorsal views of a larva of *Limnodynastes salmini* at stage 34. Scale bar = 10 mm

in lateral view with an anteriorly projecting oral disc. The nares are dorsolateral and not raised. Moderately large eyes are dorsolateral. The spiracle is sinistral and attached to the body wall along its medial edge. It is short, opening slightly dorsally and visible when viewed from above. Its diameter is constant along its length.

The anal tube is broad and opens medially. The tail fins are gently arched and rounded terminally. The dorsal fin commences posteriorly to the body and is deepest about halfway along its length. The anal tube is broad and opens medially. The ventral fin commences posteriorly to the body and is deepest about half way along its length. Tail musculature is thick tapering to a point posteriorly. Neuromast cells of the lateral line are well differentiated (Fig. 12) and extend from behind the eye, along the canthus rostralis and over the end of the snout (one sequence) and along the loreal region and under the eye (second sequence).

The mouth is anteroventral. The oral disc comprises a horny beak of moderate proportion and there are four

to five upper and three lower rows of labial teeth (Fig. 13). The most anterior upper row and the two most posterior lower rows are undivided. Labial papillae are interrupted anteromedially but extend laterally and posteriorly around the oral disc.

The dorsal surface of the body and the tail musculature and fins are heavily suffused with melanophores.

Larvae reached stage 36 by 7.ii.1991 and stage 39 by 10.ii.1991. Stage 41 was reached by 12.ii.1991 and the species had fully metamorphosed by 5.iii.1991, 43 days after spawning.

Measurements of developmental stages are given in Table 2.

Chondrocranium (Stage 34 larva, based on UAZ B1736) (Fig. 14)

Neurocranium approximately T-shaped box comprising anterior braincase and posterolateral spherical otic capsules. Large ovoid frontoparietal fontanelle exposes braincase dorsally bounded by orbital cartilages laterally and by tectum synoticum

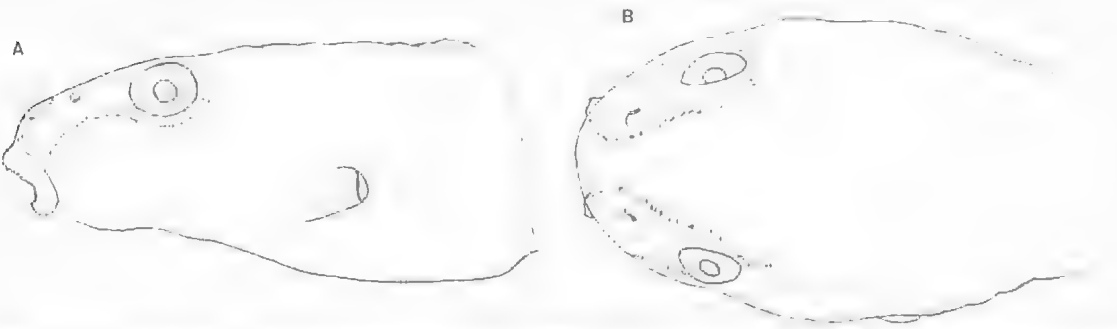


Fig. 12. A. Lateral and B. dorsal views of a larva of *Limnodinastes salmini* at stage 34 showing location of the neuromast cells of the lateral line system. Scale bar = 5 mm

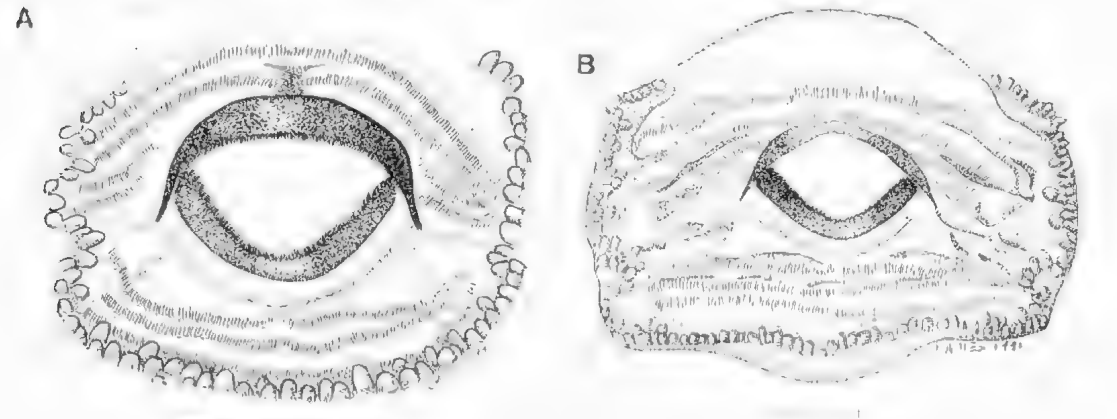


Fig. 13. A. Oral disc of larva of *Limnodinastes convexusculus* at stage 36 and B. of *L. salmini* at stage 34. Scale bar = 1 mm.

posteriorly. Narrow ethmoid plate forming anterior margin of frontoparietal fontanelle. Ethmoid plate projecting anteriorly from neurocranium as two anterolaterally diverging moderately broad finger-like cornua trabeculae. Floor of neurocranium comprising basis cranii and planum basale. Basis cranii perforated by paired foramina caroticum primarum. Posteriorly planum becoming confluent with otooccipital arch and perforated by notochord.

Massive approximately L-shaped palatoquadrate. Processus descendens (attachment to neurocranium) widening laterally to form arcus subocularis separated from basis cranii by oval subocular fenestra. Medial processus ascendens overlain dorsally to about half its width by anterior extremities of otic capsules. Arcus subocularis curving laterally while sloping ventrally. Anterolateral edges bearing low crest, becoming progressively higher and confluent with broad

processus muscularis quadrati. Arcus subocularis attached anteriorly to neurocranium by commissura quadratocranialis anterior. Finger-like projections extending ventromedially into subocular foramen.

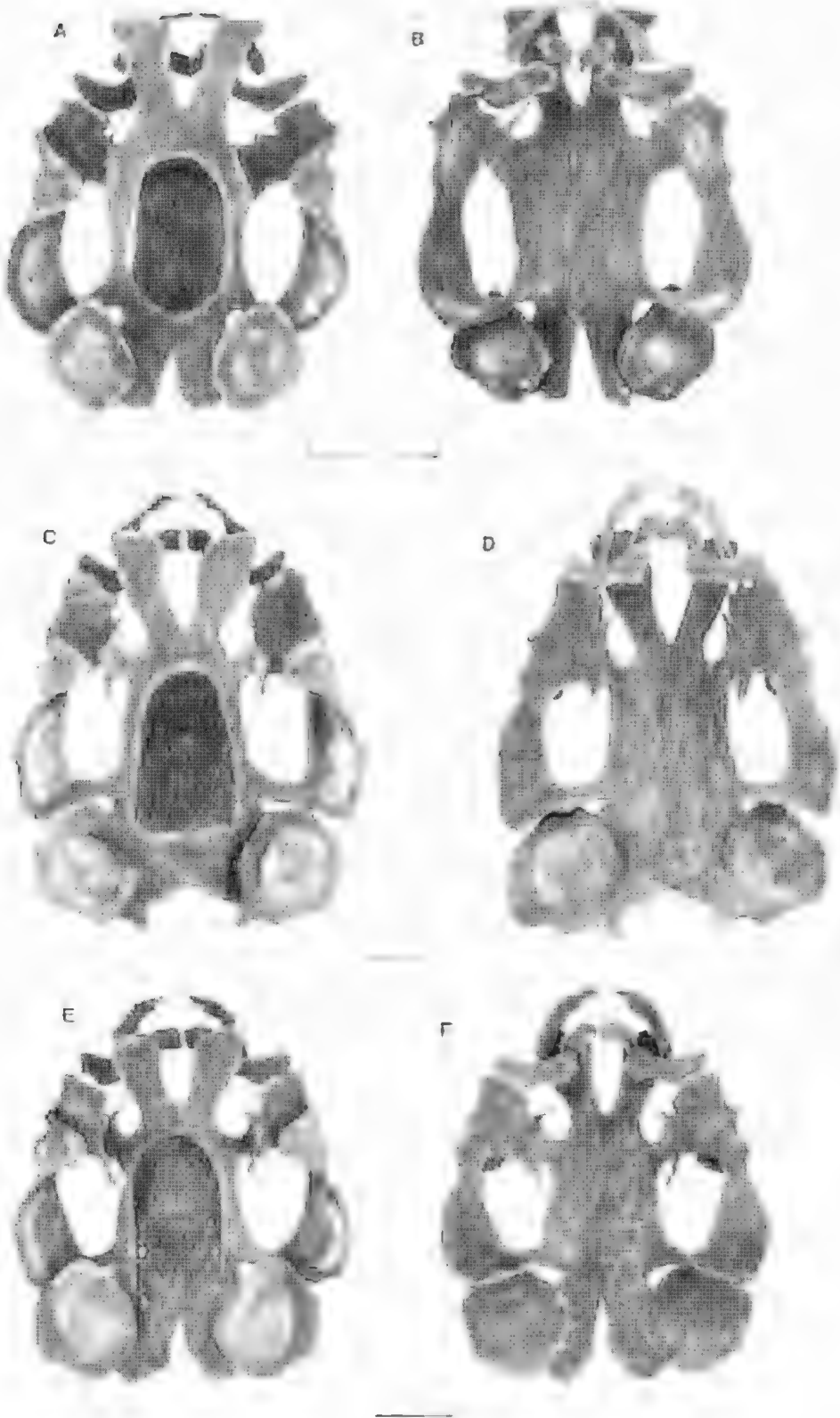
Processus muscularis quadrati inclined medially, bound to laminorbitonasalis by non-chondrified ligamentum (cartilago) tectum forming tunnel with commissura quadratocranialis anterior through which pass M. levator mandibulae posterior and M. l. m. anterior.

Processus articularis quadrati of palatoquadrate extending anteriorly from processus muscularis quadrati and articulating ventrolaterally with slightly curved Meckel's cartilage.

Ligamentum quadrati ethmoidale attaching laterally about half-way along cornua trabeculae. Dorsomedial edges of Meckel's cartilages attaching with small shallow infrarostral cartilages which form shallow

TABLE 2. Meristic data on developing *Limnodonastes salmomi*. *n* = number of individuals, \bar{x} = mean

Age, days and dates	Stage	Body length \bar{x} , range in parentheses	Total length \bar{x} , range in parentheses	n
4, 25.i.1991	24	3.35 (3.2-3.44)	8.59 (8-8.72)	11
7, 28.i.1991	25	4.64	9.2	1
6-8, 7-19.i.1991	26	5.24 (4.6-6.1)	13.42 (11.6-16.4)	23
6-7, 27-28.i.1991	27	5.67 (4.96-7.04)	13.01 (12.16-16.96)	13
15-30, 5-20.ii.1991	28	7.17 (6.2-8.16)	18.00 (12.3-19.14)	10
41-46, 31.i.-5.ii.1991	29	7.93 (6.5-8.5)	20.41 (18.0-22.2)	11
44-56, 3-15.ii.1991	30	8.16 (7.3-8.2)	21.86 (19.1-23.3)	5
43-56, 2-15.ii.1991	31	8.45 (7.1-10.9)	22.43 (20-27.5)	15
43-61, 2-20.ii.1991	32	8.89 (8.0-10.7)	24.16 (21.3-28.7)	10
43-59, 2-18.ii.1991	33	9.54 (8.6-10.8)	25.05 (23.3-27.6)	8
48-61, 7-20.ii.1991	34	10.8 (8.2-14.2)	29.24 (23.9-40.3)	8
43-61, 2-18.ii.1991	35	10.76 (9.4-12.1)	28.66 (25.7-32.4)	8
48-61, 7-20.ii.1991	36	11.9 (11.0-13.6)	32.2 (28.0-41.0)	6
56-61, 15-20.ii.1991	37	13.58 (11.9-15.6)	35.48 (30.8-40.0)	12
53, 12.ii.1991	38	17.4	45.6	1
53-61, 12-20.ii.1991	39	16.2 (14.7-17.4)	42.92 (39.9-48.5)	8
55-61, 14-20.ii.1991	40	18.03 (16.3-19.9)	48.43 (45.0-51.5)	4
53-61, 12-20.ii.1991	41	15.84 (13.9-18.5)	43.54 (39.4-47.4)	9
	45	16.52 (13.1-19.9)		25
	46	20.6		1



inverted U in ventral view with broad non-chondrified symphysis, elements joining to form lower jaw of tadpole.

Supraorbital cartilages forming upper jaw of tadpole projecting anteriorly ventral to cornua trabeculae and to both Meckel's cartilages and intraorals dorsally. Central corpus of supraorbital lying anteriorly to extremities of cornua trabeculae with non-chondrified medial symphysis. Alae extend to level of Meckel's cartilages laterally.

Limnodynastes convexiusculus

(Macleay, 1877)

FIGS 1-7, 9, 13-15

Limnodynastes convexiusculus Macleay, W. (1877) *Proc. Linn. Soc. N.S.W.* 2, 135-138 (136)

Limnodynastes olivaceus De Vis (1844) *Proc. Linn. Soc. N.S.W.* 4, 65-68 (66).

Phyllorhina novaeguineae van Kampen, P.N. (1909) *Nova Guinea* 9, 31-49 (36).

Type

Holotype, presumed lost, from Mawatta, Binaturi River near Daru, Papua New Guinea (as Katow) (Cogger *et al.* 1983)

Definition

A moderately large species (males 44-54 mm S-V, females 44-64 mm S-V) characterised by a prominent sacral hump, a mid-vertebral stripe, a rugose dorsum with longitudinal skin folds, an indistinct tympanum, nuptial excrescences in the form of fine spines in the male, females with well-developed flanges on first and second fingers, first finger shorter or equal to second in length, male call a resonant 'unk', deposition of eggs in a foam nest.

Description (based on SAM R41983)

Head high, slightly longer than broad (HL/HW 1.14), less than half snout to vent length (HL/S-V 0.41). Snout not prominent, rounded when viewed from above and in profile (Fig. 1). Nares dorsal in position, their distance from end of snout less than that from eye. Internarial span approximately equal to eye to naris distance (E-N/IN 0.96). Canthus rostralis poorly defined and straight. Eye moderate, diameter greater than eye to naris distance. Pupil shape vertical. Tympanum relatively small, not clearly defined, about 0.8 eye diameter (Fig. 1). Vomerine teeth in two elongate series, curved across the palate posterior to choanae; not meeting medially and extending laterally to extremities of small choanae.

Tongue broad. Fingers cylindrical. Second finger slightly fringed medial to thumb (Figs 2, 3), unwebbed. Subarticular tubercles moderately developed, rounded. Inner palmar tubercle very prominent, raised; outer divided. Nuptial excrescences in form of large ovoid group of fine spines on medial surface of thumb with small group on dorsal surface of base of second finger. Interdigital webbing absent.

Fingers in order of length $3 > 2 > 1 \sim 4$. Hind legs moderately short (TL/S-V 0.46). Toes long and cylindrical with very narrow lateral fringes. Subarticular tubercles conical and prominent; elongate ovoid inner metatarsal tubercle; outer metatarsal tubercle absent. Toes unwebbed other than basal fringing (Fig. 3). In order of length $4 > 3 > 5 > 2 > 1$.

Dorsum rugose with pale mid-vertebral stripe. Pelvic region humped (Fig. 1). Chocolate-coloured, well defined markings of elongate or small circular shapes trending as dorsolateral anteroposterior patterns.

Body and limbs with numerous very small conical black spines; not prominent on lateral side of head and on eyelids; on mandible, posterior portion of body, lateral surface of forearms, dorsal and lateral surfaces of legs and plantar surface of foot.

Ventral surface smooth, cream; throat speckled with pigment. Well-developed supralabial gland (Fig. 1)

Variation

The hind legs are moderately short, TL/S-V mean 0.43, range 0.38-0.47. The head is longer than broad in most specimens (HL/HW mean = 1.11, range 0.98-1.23) and is less than half the snout to vent length (HL/S-V mean = 0.38, range 0.33-0.41). Eye to naris distance is usually less than internarial span (E-N/IN mean = 0.93, range 0.77-1.14)

The small group of fine spines on the dorsal surface of the base of the second finger associated with the nuptial excrescence in the described specimen was not observed in any other material; the nuptial excrescences being confined to the medial surface of the thumb. Females have well-developed flanges on opposite surfaces of the thumb and second fingers (Fig. 2).

The dorsum varies in tubercularity and can be more or less tubercular than described. A degree of regularity in back patterning between specimens is evident. The conical spines on the dorsum are less developed in some specimens and the inner palmar tubercle is extremely well developed in some male frogs.

Material examined

Northern Territory: UAZ B1738-9 Jabiru, SAM R41979 Baralil Ck nr Jabiru, SAM R41973 Darwin (northern suburbs), UAZ B1773 Radon Ck Rd (nr Mt Brockman), SAM R41974 17 km E Jen Roper River Rd/ Stuart Hwy, Darwin, SAM R41971-2, UAZ B1728 Snake Bay Swamp, Melville Island.

Western Australia: SAM R41980-83, Mitchell Plateau (upstream from Crusher site), SAM R41984-5, Mitchell Plateau campsite, SAM R41978, Kununurra, SAM R41977 Parry Ck Rd Kununurra.

Queensland: SAM R41975-6 Edward River Township, QNPWS A393 Sugar Cane Creek, Tully Mission Beach Rd, A395-6 Kurramine, Murdering Point, N2641-2, N2659 Bamaga (Cape York), N2633

Fig. 14. Dorsal and ventral views of the chondrocranium of A, B, *Megistolotis lignarius*, stage 27; C, D, *Limnodynastes convexiusculus* Stage 30; and E, F, *L. alpinus* stage 34. Scale bar = 1 mm

Somerset (tip Cape York), UAZ A1774, N15408-9, N28030 Townsville Town Common, N33523 Pine River Bay nr Weipa.

Osteology (based on UAZ A165, B1728) (Fig. 4)

Skull well ossified. Sphenethmoid moderately ossified, in bony contact with nasals extending half length of orbit in ventral view. Preotic fused with exoccipital. Exoccipital not ossified dorso- or ventromedially. Ossification of otic region reduced ventrally. Crista parotica short and stocky, not articulating laterally with expanded otic ramus of squamosal. Frontoparietal fontanelle very poorly exposed. Frontoparietal well ossified; anterior extremities extending $\frac{1}{4}$ length of orbit (about half length ossified portion dorsal sphenethmoid). Orbital edges of frontoparietals straight, not angled posterolaterally. Anterior margins of frontoparietal fontanelle formed by sphenethmoid about halfway along length of orbit. Posterior margin masked by juxtaposition of medial margins of frontoparietals. Nasals moderately well ossified, crescentic anteriorly, overlying sphenethmoid along posteromedial extremities and with well-developed broad maxillary process in long contact with well-developed preorbital process of pars facialis of maxilla. Palatines broad, complete, running beneath dentigerous processes of vomers and overlying ventral sphenethmoid medially. Parasphenoid robust. Cultriform process urn shaped, moderately broad extending about $\frac{1}{4}$ length of orbit. Alae broad, expanded slightly laterally and angled slightly posterolaterally.

Pterygoid robust. Anterior ramus long, in short contact with moderately well-developed pterygoid process of palatal shelf of maxilla. Medial ramus moderately long, subacuminate, not overlying alae of parasphenoid. Posterior ramus extremely robust. Junction of three rami extremely robust.

Quadratojugal robust and entire. Squamosals moderately robust with moderately long zygomatic ramus and short, expanded otic ramus. Maxilla and premaxilla dentate. Pars facialis of maxilla deep with well-developed preorbital process.

Alary process of premaxilla broad, bifurcate dorsally, directed posteriorly. Posterior process of premaxilla moderately long, straight along anteromedial edges, then curved posteromedially. Palatal shelf well-developed, with moderately well-developed pterygoid process. Vomers reduced medially with extremely long dentigerous processes. Columella curved and bony.

Pectoral girdle arciferal and robust. Slender bony omosternum with stalked knobbed cartilaginous anterior extension. Broad xiphisternum. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, moderately separated medially. Scapula bicapitate, robust. Suprascapula about $\frac{1}{4}$ ossified. Anteroproximal crest of humerus moderately well developed.

Carpus of five elements. Pairs of sesamoids at junctions of metacarpals and proximal phalanges and other junctions between phalanges except terminal ones. Lateral flange on first metacarpal (Fig. 5).

Seven procervical non-imbricate presacral vertebrae. Vertebrae I and II fused. Relative widths of transverse processes:

$$\text{III} > \text{IV} > \text{SD} > \text{II} > \text{V} > \text{VI} - \text{VII} - \text{VIII}$$

Sacral diapophyses poorly expanded. Iliia extend slightly anteriorly to sacral diapophyses. Urostyle crest approximately half length of urostyle.

Slender ilial crest. Dorsal prominence prominent (Fig. 6). Dorsal protuberance lateral. Three tarsal elements in foot. Prehallux large, wedge-shaped with bony base and narrow dorsal cartilaginous edge.

Hyoid plate wider than long. Posterior processes broad and truncated. Anterior processes slender, expanded and truncated distally. Short anteromedial processes of anterior hyale. Posterior cornua ossified (Fig. 7).

Variation

Variation exists in the degree of ossification of the sphenethmoid which can be slightly greater or less than illustrated. In one specimen (UAZ B1728), a large male, the posteromedial process of the nasal is more extensive, overlying the sphenethmoid and almost reaching the anterior extremities of the frontoparietals.

The length of the dentigerous processes of the vomers may be slightly longer than those illustrated.

Material examined

UAZ A165 no data. A233 sex unknown Kununurra. B1728 male Melville Island. B1738 male Jabiru. B1739 male Jabiru. B1230 stage 34 larva. B1504 stage 30 larva. B1773 Radnor Creek Rd nr Mt Brockman. A1774 Townsville Town Common.

Habitat

Limnodynastes convexiusculus calls from small hollows, crab holes, among long grass and dense vegetation in grassland, culverts and swamps (Tyler *et al.* 1983; Davies, Martin, Tyler and Watson unpubl. observations).

Advertisement call

The advertisement call of *L. convexiusculus* is a well-tuned, single note (mean duration 74.7 ms, Table 1) repeated regularly in long calling-sequences. Call repetition rate for the six individuals reported here was 2.14 (range 1.59–2.57) calls/s (at an effective temperature of 28.0°C). Waveform and spectrographic displays of a single note and a power spectrum are shown in Fig. 15.

Distribution

Limnodynastes convexiusculus has a distribution across the north of Australia in the wet/dry tropics and including southern New Guinea (Fig. 9). The species is confined to the Kimberley region in Western Australia and occurs as far south as 34 km S Delamere Highway/Victoria Highway Jcn in the Northern Territory and Eurimbulah N.P. near Miriamvale in Queensland.

Life history

Eggs are pigmented and laid in a foamy egg mass. Tyler *et al.* (1983) described the tadpoles of *L. convexiusculus* as being an intense black with long, deep tail fins. There are four or five upper and three lower rows of labial teeth. The first upper and the first two lower rows are divided. The oral disc is surrounded by a single row of labial papillae which are interrupted anteriorly (Fig. 13). The full life history of this species has not been described.

Chondrocranium (stage 33 larva, based on UAZ B1531) (Fig. 14)

Neurocranium approximates T-shaped box comprising anterior braincase and posterolateral spherical otic capsules. Large ovoid frontoparietal fontanelle exposes braincase dorsally, bounded by orbital cartilages laterally and by tectum synoticum posteriorly. Narrow ethmoid plate forming anterior margin of frontoparietal fontanelle. Ethmoid plate projecting anteriorly from neurocranium as two anterolaterally diverging, moderately broad, finger-like

cornua trabeculae. Floor of neurocranium comprising basis cranii and planum basale. Basis cranii perforated by paired foramina carotica primaria. Posteriorly planum becoming confluent with otoccipital arch and perforated by notochord.

Massive approximately L-shaped palatoquadrate. Processus descendens (attachment to neurocranium) widening laterally to form arcus subocularis, separated from basis cranii by oval subocular fenestra. Medial processus ascendens slightly overlain dorsally by anterior extremities of otic capsules. Arcus subocularis curving laterally and sloping ventrally. Anterolateral edges bearing low crest, becoming progressively higher and confluent with broad processus muscularis quadrati. Arcus subocularis attached anteriorly to neurocranium by commissura quadratocranialis anterior. Finger-like projections extending ventromedially into subocular foramen.

Processus muscularis quadrati inclined medially, bound to lamina orbitonasalis by nonchondrified ligamentum (cartilago) tectum, forming tunnel with

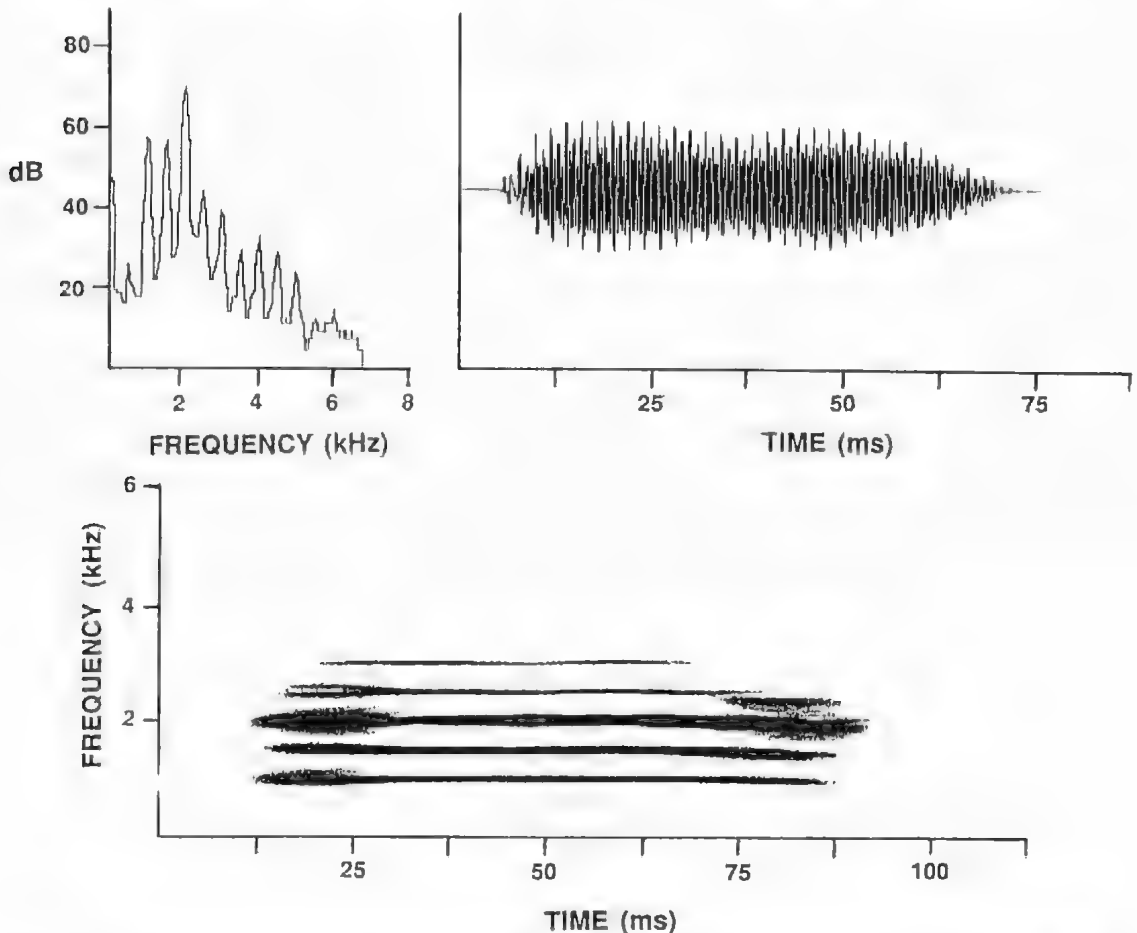


Fig. 15. Power spectrum, waveform and sonagram (sampling frequency 59 Hz) of the advertisement call of *Limnodynastes convexiusculus*. Note that the ordinate for the waveform display is not labelled because it depicts a relative linear scale in volts.

commissura quadrato cranialis anterior through which pass M. levator mandibulae posterior and M.L.m. anterior.

Processus articularis quadrati of palatoquadrate extending anteriorly from processus muscularis quadrati and articulating ventrolaterally with slightly curved Meckel's cartilage.

Ligamentum quadrati ethmoidale attaching laterally midway along cornua trabeculae. Dorsomedial edges of Meckel's cartilages attaching with infrastral cartilages. Infrastral cartilages small, forming shallow inverted U in ventral view with broad non-chondrified symphysis, elements joining to form lower jaw of tadpole.

Suprastral cartilages forming upper jaw of tadpole projecting anteriorly ventral to cornua trabeculae and dorsal to both Meckel's cartilage and infrastrals. Central corpus of suprastral lying anterior to extremities of cornua trabeculae giving appearance of paired structure with non-chondrified medial symphysis. Lateral alae extending to level of Meckel's cartilage laterally.

Megistolotis lignarius

Tyler, Martin & Davies, 1979

FIGS 1-7, 9, 14, 16

Megistolotis lignarius Tyler, M. J. Martin, A. A. & Davies, M. (1979) *Aust. J. Zool.* 27, 135-150.

Type

WAM R58299 Lake Argyle-Kununurra Rd. 6.5 km N Lake Argyle Tourist Village, Lake Argyle, Kimberley Division, W.A.

Definition

A moderate-sized species (males 43-62 mm S-V, females 47-61 mm S-V) characterised by a large and prominent tympanum (approximately the size of the eye) (Fig. 1), male nuptial excrescences consisting of small clusters of large conical black spines, females with moderately developed flange on the medial side of the second finger, first finger longer than second, advertisement call consisting of a soft regularly-repeated 'lap', eggs deposited in a foam nest.

Description

We have little to add to the comprehensive description of Tyler *et al.* (1979). However, in five females reared from the original spawn clump we recorded moderately developed flanges on the medial surface of the second finger, a character absent from the paratype material (Fig. 3).

Osteology (based on UAZ A1742) (Fig. 4)

Skull moderately well ossified, in bony contact with nasals and extending half length of orbit in ventral view. Prootic fused with exoccipital. Exoccipital not fused dorso- or ventro-laterally. Ossification of prootic reduced ventrolaterally. Crista parotica moderately long and slender, not articulating laterally with short, very poorly-expanded otic ramus of squamosal. Frontoparietal fontanelle moderately to well exposed, extending about

half length of orbit anteriorly. Orbital edges of frontoparietals straight, not angled posterolaterally. Anterior margins of frontoparietal fontanelle formed by sphenethmoid about halfway along length of orbit. Posterior margin undefined. Nasals slender, poorly ossified. Maxillary process acuminate, widely separated from moderately-developed preorbital process of pars facialis of maxilla. Palatines broad, not expanded laterally, overlap about halfway along length by lateral $\frac{1}{4}$ of dentigerous process of vomer. Parasphenoid robust. Cultriform process moderately broad, alae not quite horizontal, not expanded laterally.

Pterygoid robust, not in contact with poorly-developed pterygoid process of maxilla. Medial ramus long, moderately slender, acuminate; posterior ramus moderately stocky; bones expanded at junction of three rami.

Quadratojugal robust and complete. Squamosal moderately robust with short slender zygomatic ramus and short slightly expanded otic ramus. Maxilla and premaxilla dentate, teeth extending past pterygoid process of palatal shelf. Pars facialis of maxilla moderately deep with moderately well-developed preorbital process.

Alary processes of premaxilla broad at base, slender laterally, directed posteriorly. Palatine processes widely separated, slightly angled posteromedially. Palatal shelf poorly developed. Vomers entire, widely separated medially. Dentigerous process elongate, crescentic, behind choanae. Columella bony, curved.

Pectoral girdle arciferal and robust. Well-developed omosternum and xiphisternum. Clavicles poorly separated medially. Coracoids widely separated medially. Suprascapula $\frac{2}{3}$ ossified. Well-developed humeral crest.

Phalangeal formula of hand 2.2.3.3. Carpalia appear to be fused with Os centrale postaxiale. Very bony prepollex with spine anteromedially. Metacarpal I elongate with mediolateral flange (Fig. 5). Pairs of sesamoids at junctions of metacarpals and proximal phalanges and proximal phalanges and next phalanges.

Seven procoelous non-imbricate presacral vertebrae. Relative widths of transverse processes:

$$\text{III} > \text{SD} > \text{IV} > \text{II} > \text{V} = \text{VI} = \text{VII} = \text{VIII}$$

Urostyle crest extending $\frac{2}{3}$ length of element. Ilium with short slender crest. Prominent dorsal prominence (Fig. 6), posterolateral protuberance. Phalangeal formula of foot 2.2.3.4.3. Two tarsal elements. Terminal phalanges knobbed.

Hyoid plate wider than long. Posterior processes slender and rounded distally. Anterior processes slender slightly expanded distally. Anteromedial processes of anterior hyale expanded and broadly truncated distally (Fig. 7). Posterior cornua short and ossified.

Variation

Variation occurs in the ossification of the sphenethmoid and crista parotica in the material examined. Maximal ossification of both these elements

is as illustrated although slight ossification of the nasal capsules was noted in UAZ A1741. In this specimen also, the gap between the extremities of the dorsal crista parotica and the otic ramus of the squamosal was slightly less than shown.

Material examined

Northern Territory: UAZ A228 Cannon Hill, A588 male, B1236 larvae stage 27, B1237 larvae stage 37 Birudu.

Western Australia: UAZ A248, A1768 sub adult, A1769, A398-400 males, B428 B1771-72 females, laboratory reared from spawn from type locality, B17410, B1742 males no data.

Habitat

We have encountered a number of *M. lignarius* since the species was described and all have been true to the habitat description of Tyler *et al.* (1979).

Distribution

The species is confined to the escarpment country of the Kimberley and northern Northern Territory as defined by Tyler *et al.* (1979).

Advertisement call

The advertisement call of *M. lignarius* is a relatively poorly-tuned, single note (mean duration 26.6 ms, Table 1) repeated regularly in long calling sequences. Call repetition rate for the two individuals reported here was approximately 1.56 calls/s. Waveform and spectrographic displays of a single note and a power spectrum are shown in Fig. 16.

Life history

Tyler *et al.* (1979) described the complete life history of this species. Tadpoles are lotic with mouthparts adapted to fast flowing water and are characteristically heavily pigmented. They actively select areas of streams in which water is fast-flowing over riffles and avoid the calmer pond areas (Davies, Watson and Williams unpubl. data). There are five upper and three lower rows of labial teeth. The two most anterior upper rows and the three lower rows are undivided. Labial papillae are arranged in a double row around the oral disc and are interrupted anteromedially.

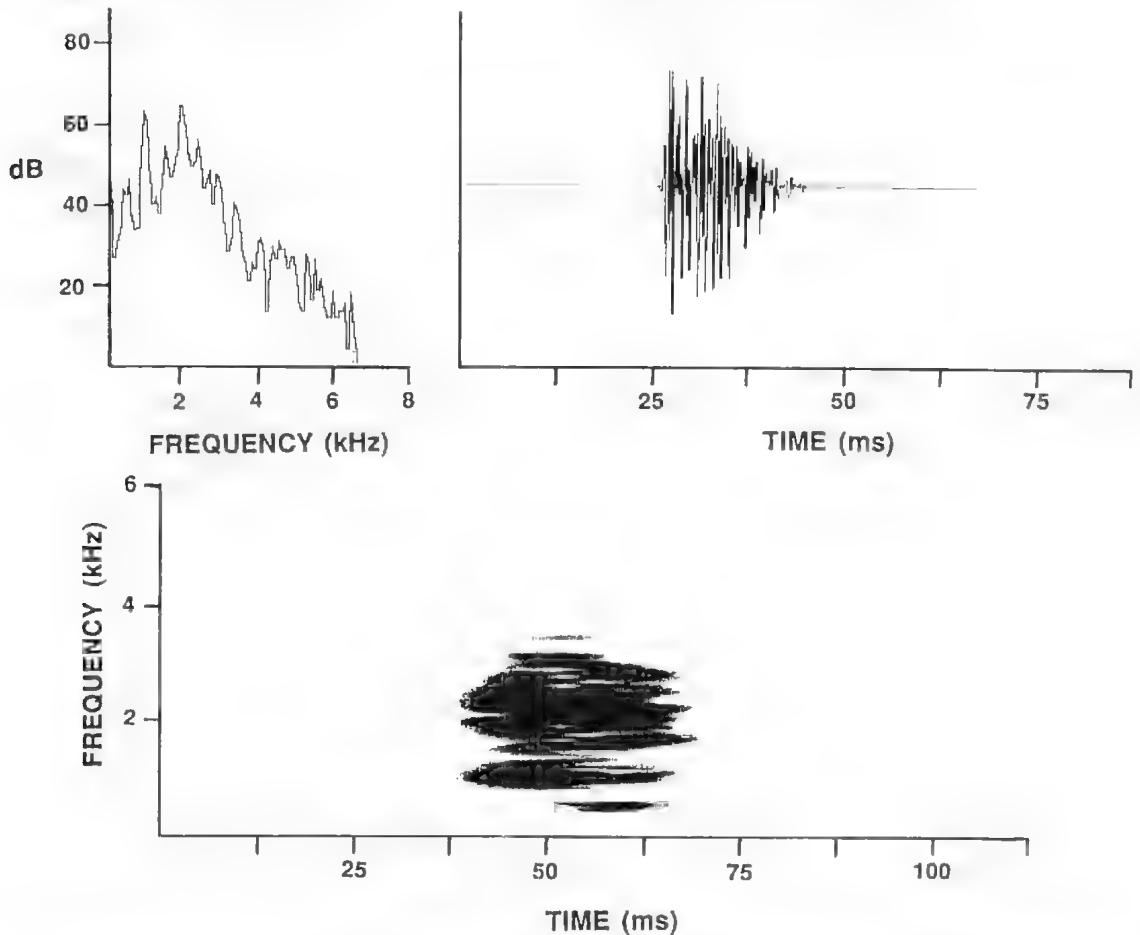


Fig. 16. Power spectrum, waveform and sonagram (sampling frequency 59 Hz) of the advertisement call of *Megistolotis lignarius*. Note that the ordinate for the waveform display is not labelled because it depicts a relative linear scale in volts.

Chondrocranium (Stage 27 larva, based on UAZ B1236) (Fig. 14)

Neurocranium approximates T-shaped box comprising anterior braincase and posterolateral spherical otic capsules. Large ovoid frontoparietal fontanelle exposes braincase dorsally, bounded laterally by orbital cartilages and posteriorly by tectum synoticum. Narrow ethmoid plate forming anterior border of frontoparietal fontanelle. Ethmoid plate projecting anteriorly from neurocranium as two elongate anterolaterally diverging, finger-like, cornua trabeculae.

Floor of neurocranium comprises basis cranii and planum basale. Basis cranii perforated by paired foramina carotica primaria. Planum becomes confluent posteriorly with otoccipital arch and is perforated by notochord.

Massive approximately L-shaped palatoquadrate. Slender processus ascendens (attaching palatoquadrate to neurocranium) widening laterally to form arcus subocularis, separated from basis cranii by oval subocularis fenestra. Medial processus ascendens

extensively overlain dorsally by anterior extremities of otic capsules. Arcus subocularis curving laterally while sloping ventrally. Anterolateral edge bearing low crest, becoming progressively higher and confluent with broad processus muscularis quadrati. Arcus subocularis attached anteriorly to neurocranium by commissura quadrato cranialis anterior. No finger-like projections of element extending ventromedially into subocular foramen.

Processus muscularis quadrati inclined medially, bound to lamina orbitonasalis by nonchondrified ligamentum (cartilago) tectum, forming tunnel with commissura quadrato cranialis anterior through which pass M. levator mandibulae posterior and M.l.m. anterior.

Processus articularis quadrati of palatoquadrate extends anteriorly from processus muscularis quadrati and articulates ventrolaterally with slightly curved Meckel's cartilage. Anterolaterally, ligamentum quadratoethmoidale attaches laterally to cornua trabeculae about one third along its length.

TABLE 3. Variation in morphological, osteological, developmental and behavioural characteristics of *Limnodynastes salmini*, *L. convexiusculus* and *Megistolotis lignarius*. Karyotypic data are from Mahony & Robinson (1986).

Character	<i>L. salmini</i>	<i>L. convexiusculus</i>	<i>M. lignarius</i>
Morphology			
Nuptial pad, spiny	—	fine	large
Spines on skin	—	+	+
Glandular dorsum	+	+	—
Tympanum	mod. distinct	indistinct	very distinct
Flanged fingers in female	present	well developed	present
Relative finger lengths	$3 > 1 > 2 = 4$	$3 > 2 \geq 1 = 4$	$3 > 1 > 2 > 4$
Karyotype (2n)	22	24	24
NOR (chromosome number)	2	11	12
Osteology			
Nasals approx. triangular	+	+	—
Frontoparietal fontanelle exposure	poor	poor	moderate
Double tooth row on vomers	—	—	+
Rel. of pars facialis with maxillary process of nasals	+	+	—
Robust join of pterygoid rami	+	+	—
Rel. anterior ramus of pterygoid and maxilla	+	+	—
Mod. slender cultriform process	—	—	+
Hastate prehallux	+	—	—
Carpalia	+	+	—
Double sesamoids on fingers	—	+	+
Developmental			
Highly melanic larvae	—	+	+
Heavily pigmented eggs	+	+	—
Larval type	lentic	lentic	lotic
Larval mouth	1,4/4:1/1,2	1,3/3:1/1,2	2,4/4:3
Cornua trabeculae extending over mouth cartilages	—	—	+
Behaviour			
Calling site	swamp	swamp	Rocky stream
Well-tuned call	+	+	—
Rifle-seeking larvae	—	—	+

Dorsomedial edge of each Meckel's cartilage attaches with infrarostral cartilages which form shallow U in ventral view with conjoined broad, non-chondrified symphysis. Cartilages form lower jaws of tadpoles.

Suprastroral cartilage form upper jaw and project ventrally to level of anterior extremities of cornua trabeculae; posteriorly do not reach level of Meckel's cartilages dorsally. Central corpus of suprastroral lies between extremities of cornua trabeculae; appears to be paired, narrow medial non-chondrified symphysis.

Lateral alae just extending to level of Meckel's cartilage laterally.

Discussion

Table 3 consolidates those characters showing variation between the three taxa. However, this is a phenetic comparison and as such does not clarify the relationships between the taxa, which await a cladistic study of the genus *in toto* with appropriate outgroups (Davies in prep.).

Information on call characteristics generally have not been included in phylogenetic analyses, although these data are of particular interest. The advertisement calls of all three species described here appear to be of similar harmonic structure (Figs 8, 15, 16). It is not clear how calling frogs produce such frequency spectra, although most interpretations suggest that the vocal cords generate a carrier frequency which is modified by secondary pulsing (amplitude modulation) that results in a pattern of side bands of the dominant frequency (Walkins 1967; Ryan 1988). Alternatively, males may produce a fundamental frequency with associated harmonics, with one or more of these harmonic frequencies being emphasised by the resonance characteristics of the body cavities. In either case, well-tuned calls produce a distinctive spectral structure, and this pattern is particularly clear in the calls of *L. convexifasciatus* and *L. salmini*, where the fourth frequency band contains most energy (Table 4, Figs 8, 15). Despite the overall structural similarity of the calls of these two species, there is a clear-cut

difference of 400-500 Hz in the dominant frequencies (Table 3). In anurans, such differences in frequency are commonly inversely related to the body sizes of calling males (Schneider 1988) and, in this case, are consistent with the overall trend in male body size in the species with *L. sahnli* being generally larger than *L. convexiusculus*.

The mode of production of the advertisement call of *M. lignatius* is equivocal. While sharing basic spectral similarities with the calls of the other species, the call is less well-tuned and the envelope shape is markedly different, having a rapid rise-time that is likely to generate a transient wide spread of frequencies (Rossing 1982) and to obscure the harmonic frequency spectrum (Table 4, Fig. 16). There is also a clear difference in the call characteristics of the two recorded individuals (Table 4). Individual #1 (SAM R16229) was calling in a rock crevice in a stream that, based on many subsequent observations of this species in the field (M. J. Tyler, M. Davies & G. F. Watson unpubl.), is a typical calling position. In contrast, the call of individual #2, the holotype (WAM R58229), was recorded while the male was moving in the open, a situation that has never again been encountered by us. Because of the behaviour of the holotype at the time when its call was recorded it is more likely that the call of individual #1 represents a typical call of this taxon.

Major developmental differences between the three taxa lie in the lotic nature of the larvae of *M. lignarius* as opposed to the lentic larvae of *L. convexiusculus* and *L. salmini*. Lotic adaptations in *M. lignarius* include a flattened body, strong tail musculature with relatively narrow tail fins and a relatively large ventral suctorial mouth disc. This is of a less elaborate nature than found in some lotic species (Davies 1989a).

Time to metamorphosis in *M. ligarius* is longer than in *L. salmii* (not known in *L. convexisculus*) being about 65 days as opposed to 43. Both inhabit seasonally arid areas and the difference in developmental rate probably reflects the relative permanence and depth of the aquatic habitat in which development occurs.

TABLE 4. Distribution of frequencies (Hz) within the calls of *Lamiodontastes salmii*, *L. convexusculus* and *Megistojulis lignarius*. The frequency with most energy (the dominant frequency) is underlined.

[illegible]

None of the taxa appear to have exceptional adaptations to rapid larval development, again reflecting the less ephemeral nature of the water bodies in which they spawn.

The lotic nature of the *Megistolotis* larvae is also reflected in the chondrocranium. The length of the cornua trabeculae and their relationship with the rostral cartilages differs in these lotic and lentic species. The cornua trabeculae are elongate in lotic *M. lignarius* and relatively shorter in lentic *L. salmini* and *L. convexiusculus*. This observation does not fit the generality of Sokol (1981) for lotic species of other families in which shortening of the cornua trabeculae is correlated with shifts of the mouth away from a subterminal position in lotic larvae.

Descriptions of chondrocrania of limnodynastine taxa are unavailable for comparison, the only published data on Australian species being those from the myohatrachine species *Uperoleia lithomoda* (Davies 1989b) and two species of *Pseudophryne* (Jacobsen 1968), none of which is a lotic species.

Ossification of the skull is negatively correlated with size. The large *L. salmini* has the poorest ossification and the smallest species *L. convexiusculus* has the greatest. Intuitively one would expect larger species to have stronger, more ossified skulls than smaller ones. However, the adult skeleton is the product of both ontogenetic and phylogenetic constraints (Lynch & Alberch 1985; Davies 1989b; Hanken 1992) and such a simple correlation rarely holds.

Lynch (1971) provided a diagnosis for *Limnodynastes* based on examination of the skulls of *L. dorsalis*, *L. fletcheri*, *L. peroni* and *L. tasmaniensis*. Data from the three taxa investigated here do not conform to this diagnosis in a number of features. The nasals are very small in *Megistolotis* rather than being relatively small although *L. salmini* and *L. convexiusculus* fit the diagnosis. The nasals are not in broad contact with the maxillae in *Megistolotis* and the frontoparietal fontanelle is poorly exposed in both *L. salmini* and *L. convexiusculus* as opposed to the moderate exposure defined for the genus. Lynch describes the zygomatic ramus as being as long as the otic ramus in *Limnodynastes* but the former is longer than the latter in both *L. salmini* and *L. convexiusculus*. The palatines are not narrowly separated medially in *Megistolotis* and the sphenethmoid does not extend anteriorly to the centre of the nasals in *L. salmini*. The alae of the parasphenoid are not broadly overlapped laterally by the median ramus of the pterygoids in any of the three taxa and the anterior ramus of the pterygoid does not conform to the generic description in either *Megistolotis* or *L. salmini*.

Parker (1940) discussed the relative lengths of metacarpal I in *Limnodynastes* and reported a trend towards reduction in the phalanges of the first finger.

Internally, the metacarpal bone is disproportionately long. The trend was noticed in *L. fletcheri*, *L. peroni* and to a lesser extent in *L. salmini*. Parker suggested that it is significant that these species do not have nuptial excrescences. He went on to argue that species that spawn in water, such as *Limnodynastes*, need nuptial excrescences to aid in clasping the female and that lack of the same must be compensated for in some way, i.e., by changes in the relative length of the fingers. The same trend is recorded in *M. lignarius* but this species has well-developed spinous nuptial excrescences, so does not support the assumption. Further, we record here the presence of glandular nuptial excrescences in *L. salmini* contrary to the observations of Parker (1940).

Parker (1940) provided X-rays of the hands of *L. tasmaniensis*, *L. peroni*, *L. fletcheri* and *L. salmini* to illustrate the nature of the metacarpals and digits. The material in this study for which comparable data are available are all males and all have a lateral flange on the medial surface of the first metacarpal. Examination of Parker's material shows the presence of this structure only in male *L. peroni* but not in female *L. salmini* and male *L. fletcheri*. Whether this is a sexually dimorphic character remains in doubt as the X-rays are extremely granular and may not be of sufficient quality to detect the structure.

Limnodynastes salmini and *L. convexiusculus* share similar habitats and, except for the difference in dominant frequency, have very similar calls. The distributions of these two species have a zone of overlap between Miriamvale and St Lawrence in Queensland. Identification by way of call from these areas must therefore be regarded as dubious when compiling distribution data.

The data recorded here contribute to our knowledge of the morphology and reproductive biology of three Australopapuan anurans and also will contribute to a wider analysis of the phylogenetic relationships within *Limnodynastes* Fitzinger.

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**A NEW GENUS AND SPECIES OF FROG
(ANURA: LEPTODACTYLIDAE: MYOBATRACHINAE)
FROM SOUTHERN TASMANIA**

By D. E. ROUNSEVELL, D. ZIEGELER*, P. B. BROWN*, MARGARET DAVIES†
& M. J. LITTLEJOHN‡*

Summary

Rounsevell, D. E., Ziegeler, D., Brown, P. B., Davies, M. & Littlejohn, M. J. (1994)
A new genus and species of frog (Anura: Leptodactylidae: Myobatrachinae) from
southern Tasmania. Trans. R. Soc. S. Aust. 118(3), 171-185, 30 November, 1994.

Bryobatrachus nimbus gen. et. sp. nov. is described from moist cool habitat in
southern Tasmania. The genus is distinguishable by its direct development, fusion of
presacral vertebrae VII and VIII with the sacrum, dentate maxillary arch, absence of
vomerine teeth and the presence of a columella. The species is small (males 19-27;
females 25-30 mm S-V) with distinctive dark patterns on the dorsum and an
advertisement call that is a series of "tòks" with a pulse repetition rate of 5.3-6.1
pulse/s. Eggs are laid in cavities in moss in groups of 9-14 and hatch as four-legged,
tailed froglets. *B. nimbus* gen. et. sp. nov. is cryptozoic in vegetation at poorly
drained sites on wet peat, or in edaphic moss in implicate rainforest and subalpine
moorland at altitudes from near sea level to 1,100 m. The genus and species are
endemic to Tasmania and bring the frog fauna of the island to 11 species.

Key Words: Anura, *Bryobatrachus nimbus* gen. et. sp. nov., Tasmania, new genus,
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Key Words: Anura, *Bryobatrachus nimbus* gen. et sp. nov., Tasmania, new genus, new species, morphology, osteology, advertisement call, development, habitat, cryptozoic, distribution.

Introduction

The frog fauna of Tasmania is an element of the Bassian Province of south-eastern Australia (Littlejohn & Watson 1985). As well as species with wide ranging distributions throughout eastern Australia (e.g. *Ranidella signifera* Girard, 1858 and *Limnodynastes tasmaniensis* Günther, 1858 [Leptodactylidae: Myobatrachinae and Limnodynastinae]), there are two endemic species, *Litoria butrowsae* (Scott, 1942) (Hylidae) and *Ranidella tasmaniensis* (Günther, 1864) (Leptodactylidae: Myobatrachinae).

Ten taxa are recognised in Tasmania and aspects of their biology are relatively well known (Martin & Littlejohn 1982). With a greater appreciation of the need to document the biodiversity of the continent, efforts have been directed toward surveys and the mapping of distribution patterns of local fauna. During one such project aimed at providing an atlas of the frogs of Tasmania, one of us (D.Z.) recalled having heard at several high altitude sites, a distinctive frog call that could not be attributed to any described Tasmanian taxon.

In late November 1992 calls were recorded at the Hartz Mountain National Park and specimens were collected (Robertson 1993; Rounsevell & Swain 1993).

Examination of the collection at the Tasmanian Museum and Art Gallery, Hobart, revealed further material.

The frogs could not be referred to any known genus, and so a new genus is erected to accommodate them here. We describe the species and provide information on its biology and distribution.

Materials and Methods

Material reported here is deposited in the Tasmanian Museum and Art Gallery, Hobart (TMAG), South Australian Museum, Adelaide (SAM), Museum of Victoria, Melbourne (NMV), the Australian Museum, Sydney (AM) and the Department of Zoology, University of Adelaide (UAZ).

Measurements were taken using dial calipers reading to 0.05 mm, or with an eye-piece micrometer. Measurements (mm) were: eye diameter (E); eye-to-naris distance (E-N); internarial span (IN); snout-vent length (S-V) and tibia length (TL); and for selected specimens, head length (HL) and head width (HW). The methods of measurement follow Tyler (1968) and interpretation of data follows Tyler (1978). Data are presented as means with ranges in parentheses. The tympana of many specimens are indistinct or not visible, and hence accurate measurements of head width and head length were not always possible.

Osteological data were obtained from specimens cleared and stained with alizarin Red S for bone after the method of Davis & Gore (1947), and with alizarin Red S for bone and alcian blue for cartilage after the method of Dingerkus & Uhler (1977). Osteological descriptions follow Trueb (1979), and Andersen (1978¹) for the carpus and tarsus.

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¹ ANDERSEN, M. L. (1978) The comparative myology and osteology of the carpus and tarsus of selected anurans. PhD Dissertation, Dept of Systematics and Ecology, University of Kansas (Unpubl.).

Line drawings were made with the aid of a Wild M8 stereoscopic dissecting microscope with attached camera lucida.

Most field observations were made in the spring and summer of 1993, at the type locality at Hartz Mountains National Park, and during a field survey in October and November 1993 (Ziegeler 1994). Air temperature and relative humidity were measured with a 'Zeal' whirling psychrometer (BS 2842/66).

Recordings of the advertisement calls of one individual were made with a Sony WM-D6 Pro-Walkman cassette tape recorder and a Beyer M-88 cardioid dynamic microphone by G. F. Watson at the type locality on 5 December 1992 at about 1330 hours E.S.T. The wet-bulb air temperature was 8.5°C and a dry-bulb air temperature was 9.2°C in the vicinity of the calling male.

Recordings of advertisement calls of several individuals also were made at the type locality by P. B. Brown on 30 November 1992 using a Marantz SuperScope C-205 cassette recorder and a Sennheiser MK 80 electret microphone; temperatures were not measured.

The calls were replayed on a Nakamichi Dragon cassette recorder, with the line output directed to a Kay Elemetrics DSP-5500 digital Sonar-Graph. Calls of sufficient intensity that did not overlap those of neighbours were analysed. The number of pulses in a call (determined by inspection), and measurements of call duration (ms) and pulse repetition rate (as pulses/s; from the peak of the first pulse to the peak of the last pulse) were determined from the wave-form display of each clear call.

For the six clear calls obtained by G. F. Watson, dominant frequencies (Hz) were determined from the power spectrum for the complete call, with the maximum and next highest peaks being measured. Pulse duration, and attack and decay times of the middle pulses also were estimated to the nearest millisecond (ms) from the wave-form displays. The repetition rate of the calls (as calls/min) also was determined from this sequence.

Eighteen calls from the recording sequence obtained by P. B. Brown were analysed, and duration, number of pulses and pulse rate determined. As calls of several individuals are included, the values are treated as a group.

Systematics

Four anuran families are native to Australia: Hylidae, Ranidae, Microhylidae and Leptodactylidae (Myobatrachidae of many authors). The new frog was

identified as belonging to the family Leptodactylidae, sub-family Myobatrachinae, on the basis of: (1) terminal phalanges knobbed; (2) intercalary elements absent; (3) apical element of *M. intermandibularis* absent; (4) pectoral girdle arciferous; (5) palatines discrete; (6) prepharyngeal folds absent; (7) alary processes of hyoid plate moderately broad and wing-like; (8) cricoid cartilage divided ventrally; (9) intervertebral discs not fused to centra in adults; (10) attachment of *M. intermandibularis* upon *M. submentalis* absent.

The first three characters exclude the species from the Hylidae, and the fourth excludes it from the Ranidae, whilst the first, fourth, fifth and sixth exclude it from the Microhylidae. The remaining characters are definitive of the leptodactylid subfamily Myobatrachinae (Parker 1940; Lynch 1971; Tyler 1972; Davies 1987²).

Littlejohn *et al.* (1993) report 9-12 genera as being variously recognised within the Myobatrachinae. The new species cannot be placed in any of these genera on the basis of the following combination of characters: an apparent autapomorphy of the vertebral column of fusion of the presacral vertebrae VII and VIII with the sacrum, presence of a dentate maxillary arch, the lack of vomerine teeth, presence of a columella, and direct development of the young with a four-legged, tailed froglet hatching from the egg membranes.

The frog is excluded specifically from the myobatrachine genera as follows: together with the vertebral fusion, (1) from *Asa* by the absence of parental care by the male, by the absence of vomerine teeth and by the complete phalangeal formula; (2) from *Crinia* (*sensu* Blake 1973) by the absence of vomerine teeth and the absence of a free-swimming tadpole; (3) from *Genierina* by the absence of vomerine teeth and of a projecting dorsal flange on the anterior ramus of the pterygoid, by the projecting snout and by the granular ventral surface; (4) from *Rundella* by the width of the bases of the alary processes of the hyoid, by the absence of free-swimming tadpoles and by the nature of the tymosternum; (5) from *Leptodactylus* by the absence of T-shaped terminal phalanges on the digits, by the absence of vomerine teeth and by the lack of free-swimming tadpoles; (6) from *Uperoleia* by the absence of hypertrophied dermal glands and of two raised compressed metatarsal tubercles, and by the absence of a free-swimming tadpole; (7) from *Pseudophryne* by the presence of a columella and of teeth on the maxillary arch, and the absence of a free-swimming tadpole; (8) from *Arenophryne* by the presence of a columella and of teeth on the maxillary arch, and by the absence of modified phalangeal formulae on the hands and feet; (9) from *Myobatrachus* by the presence of teeth on the maxillary arch, by the absence of a modified phalangeal formula of the hands and by the absence of reinforcement of the anterior

² DAVIES, M. (1987) Taxonomy and systematics of the genus *Uperoleia* Gray (Anura: Leptodactylidae). PhD Thesis, Department of Zoology, University of Adelaide. Unpubl.

portion of the skull by anterior placement of the nasals. (10) from *Metacrinia* by the presence of teeth on the maxillary arch, by a large omosternum, by the lack of extensive reduction of the palatines laterally, by the less extensive nasals, and by the projecting snout and shape of the head.

Genus *Bryobatrachus* gen. nov.

Type species: *Bryobatrachus nimbus*

Diagnostic definition

1. Alary processes of hyoid plate broad and wing-like. 2. Cricoid cartilage divided ventrally. 3. Intervertebral discs unfused in adults. 4. Attachment of *M. intermandibularis* on *M. submentalis* absent. 5. Hypertrophied dermal glands absent. 6. Small flattened inner metatarsal tubercle. 7. Tiny, or no outer metatarsal tubercle. 8. Snout projecting when viewed from above. 9. Maxillary arch toothed. 10. Vomers reduced to one or two fragments at edge of choanae. 11. Columella present. 12. Palatines slightly reduced laterally. 13. Nasals not located anteriorly on skull. 14. Omosternum large, mushroom-shaped with narrow stalk. 15. Phalangeal formula of hand 2,2,3,3. 16. Phalangeal formula of foot 2,2,3,4,3. 17. Terminal phalanges knobbed. 18. Vertebrae VII and VIII fused with sacrum. 20. Development direct — four-legged tailed froglet hatching from egg membranes.

Etymology

Derived from the Greek *bryon* (= moss) and *batrachos* (= frog), alluding to the habit of breeding in moss or moss-like vegetation.

Bryobatrachus nimbus sp. nov.

FIGS 1-10

Holotype: TMAG C1012, an adult male, 300 m north of Lake Esperance (146°46'E, 43°13'30"S), Hartz Mountains National Park, 920 m, collected by D. E. Rounsevell & D. Ziegeler on 18.x.1993.

Paratypes: 9 ♂♂, 3 ♀♀ and 2 s.a.: TMAG C1009, ♂, same data as holotype, except collected 1.x.1993; TMAG C1010, ♂, same data as holotype; TMAG C1013, s.a., Mt Sprent (145°58'E, 42°47'30"S), coll. D. Ziegeler, 21.x.1993; TMAG C1024, ♂, topotype, coll. P. B. Brown, 28.xii.1993; TMAG C1025, ♀, same data. C1024 and C1025 in amplexus; TMAG C350, (2 ♂♂), Mt La Perouse Base Camp, ANZSES Expedition Jan. 1984; TMAG C345, s.a., same data as C350; TMAG C869, ♂, Mt La Perouse (146°44'30"E, 43°30'20"S), rocks above Pigsty Bonds on Mt La Perouse track, 1.7 km NW of summit, coll. M. N. Hutchinson & S. Hudson, 9.ii.1990; SAM R43671 (cleared and stained), ♂, same locality as holotype, coll. D. E. Rounsevell, 25.xi.1992; SAM R43672, ♂, same data; AM R143566 (cleared and stained), ♀, same locality as holotype, coll. D. E. Rounsevell, 25.xi.1992; AM R143565, ♂, same

locality as holotype, coll. P. B. Brown & D. Ziegeler, 29.xi.1992; NMV D67310, ♂, same locality as holotype, coll. A. & J. E. Wapstra, 29.xi.1992.

Definition

A small species (males 19–27 mm S-V, females 25–30 mm S-V) characterised by a toothed maxillary arch, presence of a columella, lack of vomerine teeth, unmodified phalangeal formulae, knobbed terminal phalanges, widely exposed frontoparietal fontanelle, presacral vertebrae VII and VIII fused with the sacrum, unfringed fingers and toes, granular ventral surface, dorsum consistently marked with dark chevron-shaped mark between eyes, pair of parallel dark lines from shoulder along anterior portion of back and pair of dark patches in oocyteal region, eggs large and unpigmented, four-legged tailed froglet hatches from egg membranes, advertisement call a series of "toks" with a pulse repetition rate of 5.3–6.1 pulses/s.

Description of holotype

Maxillary teeth present; vomerine teeth absent, tongue oval, free behind; tympanum obscure. Snout short, projecting and slightly truncated when viewed from above, overshoot and sloping posteriorly when viewed in profile (Fig. 1A). Eye to naris distance less

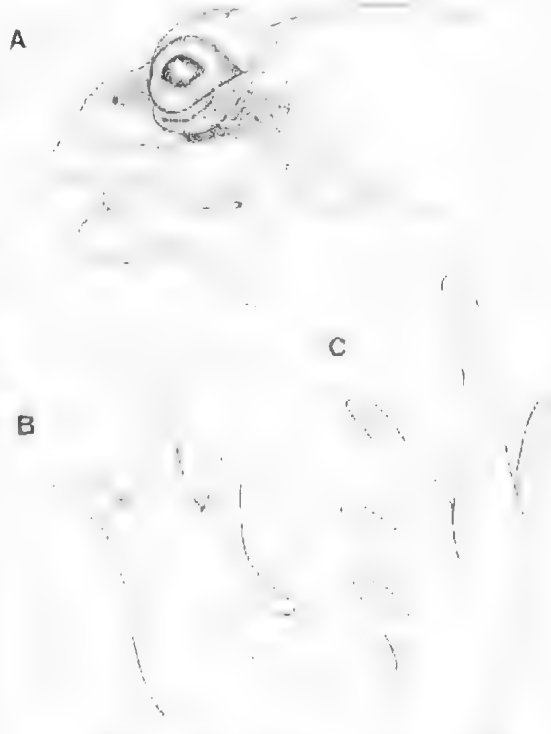


Fig. 1. *Bryobatrachus nimbus* gen. et sp. nov.: A, lateral view of the head; B, palmar view of hand; and C, plantar view of foot (Holotype, TMAG 1012). Scale bar = 5 mm.

than internarial span ($E-N/IN = 0.7$). Nares located laterally on snout, directed dorsally. Canthus rostralis straight, loreal region concave, facial shelf conspicuous. Eye prominent, pupil horizontal when constricted. Fingers short, unwebbed with flattened subarticular tubercles (Fig. 1B). Terminal discs undilated. Palmar tubercles flattened but conspicuous. Several supernumerary tubercles present; fingers in order of length $3 > 4 > 2 > 1$.

Hindlimbs short ($TL/S-V = 0.36$). Toes relatively short, unfringed and unwebbed (Fig. 1C); in order of length $4 > 3 > 5 > 2 > 1$. Small flattened inner metatarsal tubercle, and tiny rounded outer metatarsal tubercle. Subarticular tubercles small and not prominent.

Dorsal surface sparsely tubercular, tubercles linear along length. Prominent tubercles on dorsal surface of legs. Ventral surface granular with well-developed

coarsely granular pelvic patch. Small bifurcated unfringed cloacal flap.

Dorsum dark tan in preservative with chevron-shaped black mark between eyes, paired elongated black markings from scapula region, and paired moderately elongate black patches in the coccygeal region. Canthal stripe anterior to naris, through loreal region and eye to axilla. Pale patch beneath eye (Figs 1, 2).

Ventral coloration chocolate with cream speckling (Fig. 2); dark chocolate suffusion on throat. Paired vocal slits posteriorly at angle of jaw.

Colour in life

Dorsal surface shades of dark brown. Darkest brown markings distinctive varying in intensity and occurring bilaterally in pairs in the coccygeal region and in association with scapulae. Coccygeal pair lie within region of paler brown or "ground" colour, not hidden when colour intensity changes. Larger patch of dark brown occurs between scapulae and anteromedially which, when at darkest, can conceal upper pair of bilateral markings. Chevron-shaped mark of dark colour between eyes. Small white patch above cloaca. Limbs barred with dark brown. Other broad dark brown patches occur along paler brown flanks. Dorsal surface of snout and inner thighs unmarked and paler brown or "ground" colour. Paired canthal stripes from naris to flank broadest in tympanal region. Dark brown canthal stripe passes through most of the eye except uppermost part of iris. Iris dark brown below and iridescent gold above facial stripe. Lower stripe of white or cream, commencing between eye and naris and varying in width being narrowest, or with lower edge notched, below eye and including neither lower eyelid nor upper lip. Ventral surface dark brown covered with irregularly-shaped fine white spots of similar size extending over the limbs and sometimes to lower throat. Chin sometimes paler and less spotted. Pale lemon-yellow tint on paler parts of throat and forelimbs.

Dimensions (mm): S-V 22.6; TL 8.2; E-N 1.7; IN 1.4, E 2.7.

Variation

There is little variation in external morphology, other than colour pattern. The protruding snout is not as pronounced in all paratypes; in those in which it is most developed, it appears to be thickened and whitish. The legs are uniformly short ($TL/S-V = 0.35$ [0.31-0.38]), and the head usually longer than width ($HL/HW = 1.06$ [0.96-1.23, $n = 9$]). There is variability in the relationship between eye-to-naris distance and internarial span ($E-N/IN = 0.89$ [0.71-1.12]). The tympanum is obscure or indistinct

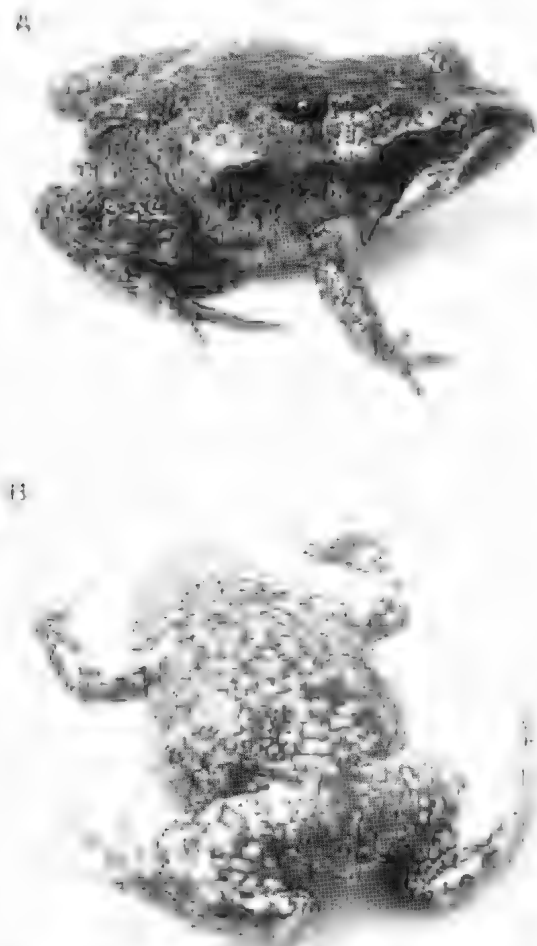


Fig. 2. *Bryobatrachus nimbus* gen. et sp. nov.: A, dorsolateral and B, ventral views in life (Paratype TMAG 1009) (Photo, J. Voss).

(Figs 1, 2). Toes are uniformly unfringed, but there is variability in development of the palmar tubercles; in TMAG C1009, these are particularly pronounced. When present, the outer metatarsal tubercle is tiny and the inner metatarsal tubercle usually flattened. A tarsal fold is present in TMAG C1010. Rugosity of the dorsum varies but is not conspicuous. Ventral granularity of the belly is variable.

The ground colour of the dorsum and the extent and nature of the markings varies. The three pairs of dark markings on the dorsum are consistently present. The markings between the eyes are chevron-shaped, whilst those in the scapular region are often lyrate and can vary in length, occasionally almost coalescing with the coccygeal pair.

Dorsal colour varies from very dark brown to grey-brown or tan, and, in darker specimens the anterior pair of markings becomes obscure and often merges with the suprascapular pair. The coccygeal pair always contrasts with the general body colour and is distinctive (Fig. 2A).

A pale or tan mid-vertebral stripe is present in several specimens, and occasionally a pale medial ventral stripe is present in paler specimens. The ventral surface can be dusky grey with white spots, or pale with dark spots. The throat is always pigmented, but added dark suffusions are present in calling males. The throat has a salmon iridescent hue in life, and a lemon coloration often occurs in the axillae. Reddish patches occur along the lower flanks and in the inguinal region. A pale spot often occurs above the cloaca.

The pale stripe beneath the dark canthal stripe of the head varies in extent, maximal development being shown in Fig. 2.

Osteology (based on SAM R43671)

Skull poorly ossified. Sphenethmoid ossified medially, with ossification extending anteriorly between the nasals dorsally and ventrally. Cartilages of nasal capsules are considerably calcified ventrally (Fig. 3). Prootic and exoccipital superficially fused by extensive calcification giving short and stocky crista parotica. Exoccipital calcified dorsomedially and ventromedially. Crista parotica not articulating with elongate unexpanded otic ramus of squamosal. Carotid canal roofed on frontoparietals medial to well-developed epiotic eminences. Occipital condyles widely separated. Frontoparietal fontanelle widely exposed for approximate length of orbit. Anterior extremities of frontoparietals extend anteriorly to anterior margin of frontoparietal fontanelle. Orbital edges of frontoparietals slightly curved and angled slightly posterolaterally. Nasals moderately well ossified, approximately triangular and widely separated medially. Maxillary process short, and widely separated from well-developed preorbital process of pars facialis of maxilla.

Palatines moderately robust, reduced slightly laterally and curving posteromedially to overlie sphenethmoid at anterior extremities of orbit. Parasphenoid moderately robust with moderately broad, deeply crenate cultriform process extending approximately $\frac{3}{4}$ length of orbit in ventral view. Alae moderately short, relatively broad, extending slightly posterolaterally, not overlain by medial ramus of pterygoid. Pterygoid robust; anterior ramus in long contact with maxilla anteriorly, and with base of squamosal shaft and with cartilaginous quadrate posteriorly. Squamosal robust, with short zygomatic

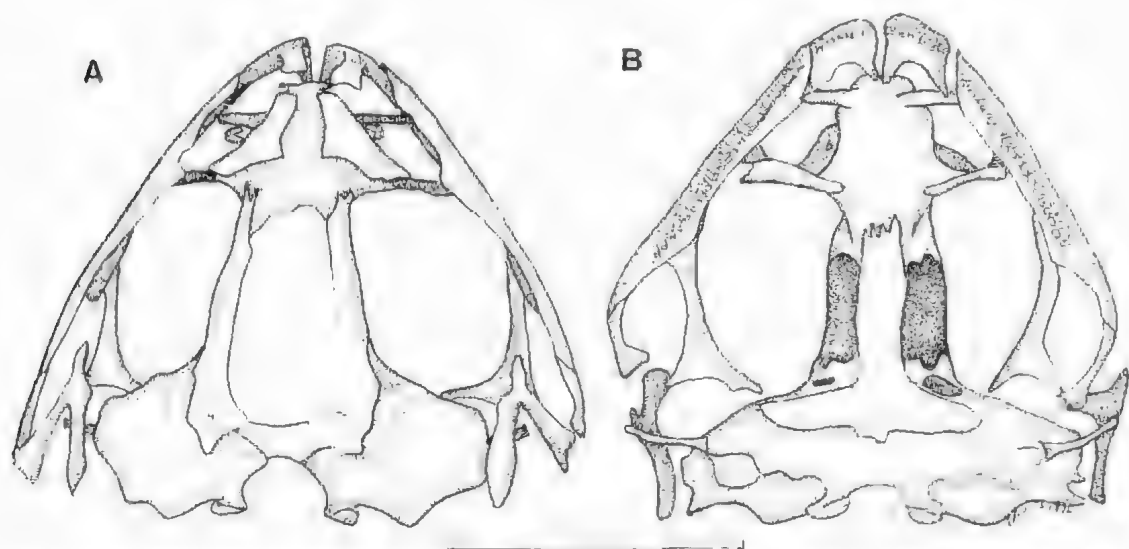


Fig. 3. *Bryobatrachus umbus* gen. et sp. nov.: A dorsal and B ventral views of the skull of SAM R43671. Scale bar = 5 mm

ramus and long unexpanded otic ramus not overlying crista parotica (Fig. 3).

Maxilla and premaxilla dentate. Palatal shelf deep with well-developed palatine processes of premaxillae not abutting medially. Well-developed pterygoid process of maxilla. Alary processes of premaxillae broad at base with narrower posterodorsal projections, slightly concave. Vomerine fragments present on edge of choanae on right hand side. Bony columella present (Fig. 3).

Pectoral girdle arciferal and robust (Fig. 4A). Omosternum large, mushroom shaped with an elongate narrow stalk; xiphisternum also large and mushroom shaped, with a short broad stalk. Some calcification of xiphisternum and epicoracoid cartilages. Sternum cartilaginous. Clavicles moderately slender, curved, poorly separated medially; coracoids robust, moderately widely separated medially. Scapula bicapitate, longer than clavicles. Suprascapula about $\frac{1}{2}$ ossified.

Eight non-imbricate procoelous presacral vertebrae. Vertebra VIII fused with sacrum and with vertebra VII. Vertebra VII fused with vertebra VIII and with sacrum (Fig. 5). Transverse processes of vertebra IV with bilateral anomaly (Fig. 5). Sacral diapophyses poorly expanded. Relative widths of transverse processes:

$$\text{III} > \text{IV} > \text{II} > \text{SD} > \text{V} > \text{VI} > \text{VII} > \text{VIII}$$

Urostyle bicondylar with dorsal crest extending approx. $\frac{1}{2}$ length. Small rounded dorsal prominence on ilium (Fig. 5). Dorsal protuberance not prominent. Iliac crest absent. Pubis calcified.

Humerus with strongly-developed deltoid crest anteroproximally. Phalangeal formula of hand 2,2,3,3. Carpus of six elements exhibiting moderate torsion. O. radiale and O. ulnare present; O. radiale larger of the two. Both elements articulate with O. radioulna proximally and with each other posteromedially. Distally, both articulate with large transversely elongated O. centrale postaxiale which articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends from lateroproximal corner. Small calcified palmar sesamoid proximally on ventral surface (Fig. 6). O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal element of O. distale carpal 2 and O. distale carpal 3 and laterally with basal prepollical element.

Carpal element of O. distale carpal 2 articulates with carpal element of O. distale carpal 3. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. Bones of approximately equal length. Two distal tarsal elements present. Lateral elements largest, lying at base of O. metatarsus III and extending laterally to articulate with

medioproximal side of base of O. metatarsus II. Second element appears to be result of fusion of two elements and lies at base and slightly lateral to O. metatarsus II, and articulates with base of O. metatarsus I and O. centrale prehallucis. Distal prehallucal element small and knobbed, calcified.

Hyoid plate longer than broad (Fig. 4C). Base of alary processes occupying $\frac{1}{3}$ to $\frac{1}{2}$ of lateral edges of hyoid plate; not pedunculate. Anteromedial processes of anterior hyale long and slender. Posterolateral processes of hyoid plate irregularly shaped, moderately long. Posterior cornua ossified.

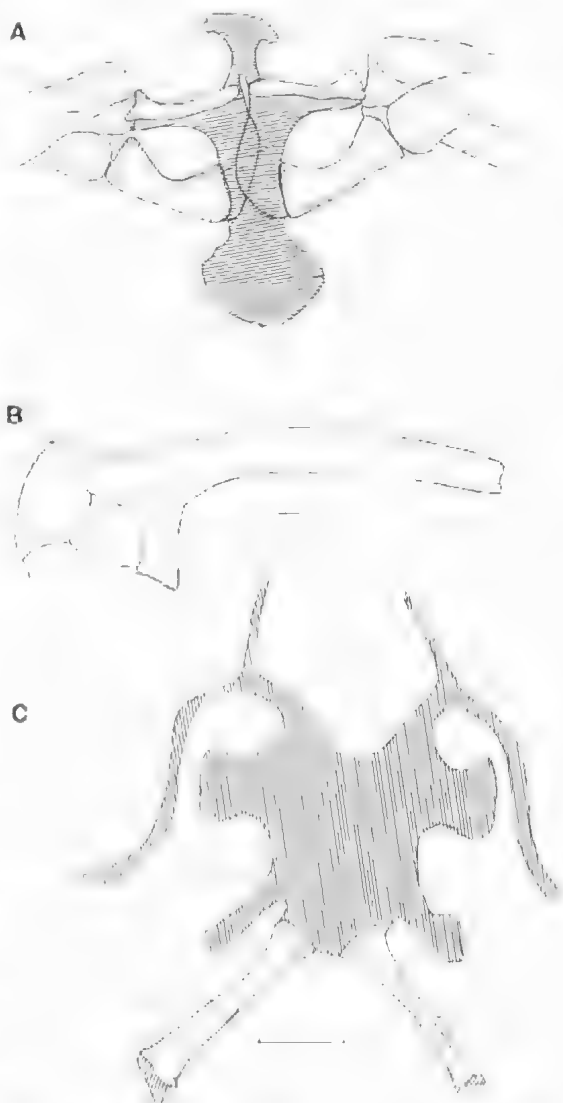


Fig. 4. *Bryobatrachus nimbus* gen. et sp. nov.: A, dorsal view of the pectoral girdle; B, lateral view of the ilium; C, ventral view of the hyoid (SAM R43671). Scale bars = 1 mm.

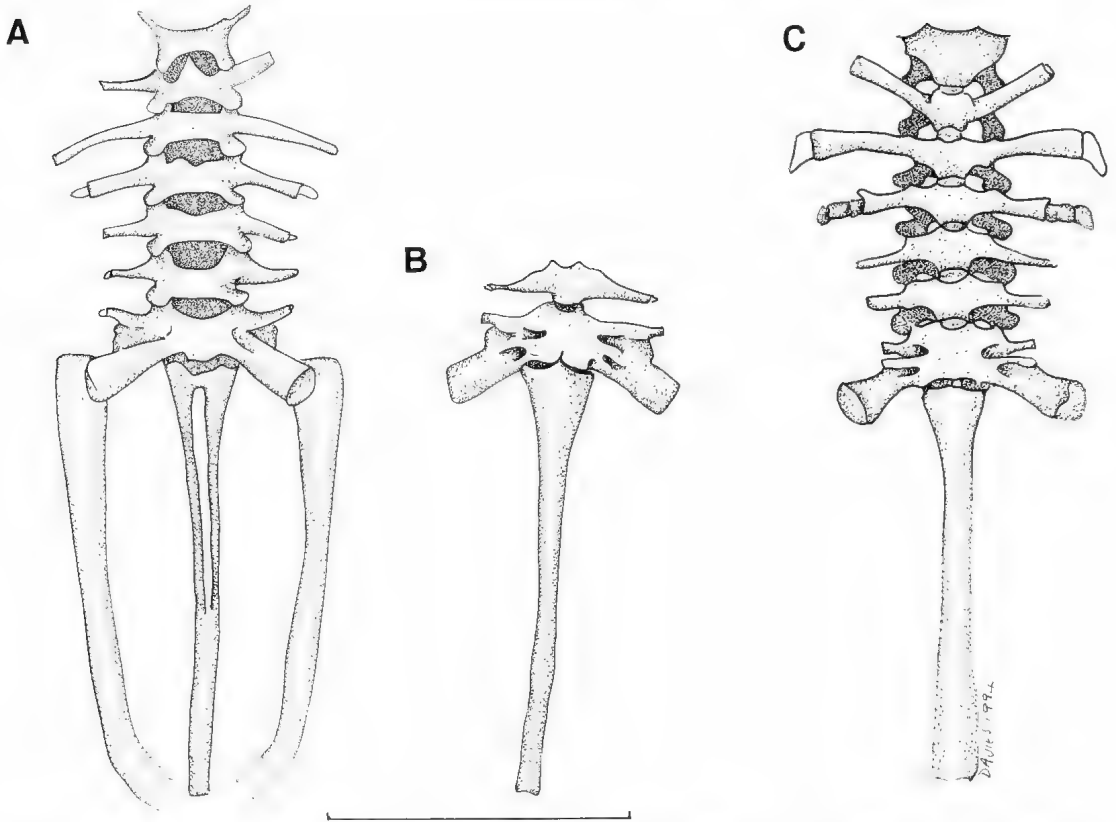


Fig. 5. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal view of the vertebral column B. ventral view of vertebrae VI, VII and VIII and the sacrum (AM R143566) and C. ventral view of the vertebral column (SAM R43671). Scale bar = 5 mm.

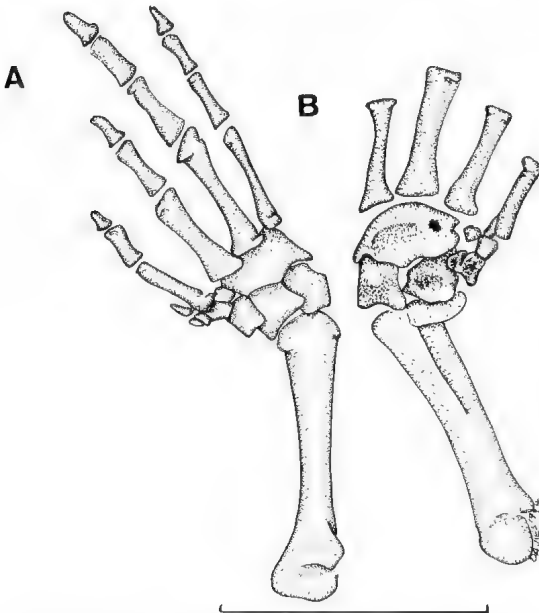


Fig. 6. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal and B. ventral views of the carpus (SAM R43671). Scale bar = 5 mm.

Variation

Paratype (AM R143566) has been cleared and stained. In comparing this specimen with the described male, it is apparent that the latter is probably a senescent specimen on the basis of the high degree of calcification lacking in the larger female specimen. For example, calcification of the nasal cartilages, of the omosternum, xiphisternum and epicoracoid cartilages, of the tiny cartilaginous prepollex and the palmar sesamoid is lacking in this specimen. In addition, there is less calcification of the crista parotica region between the exoccipitals and prootics.

Consistent with this view is the lack of ossification of the sphenethmoid between the nasals dorsally and ventrally, and the lack of fusion of the medial tarsal elements. Remnant vomerine fragments occur on the edges of both choanae in this specimen. The vertebral anomaly on the transverse processes of presacral vertebrae IV is not present, but fusion of presacral vertebrae VII and VIII with the sacrum is consistently present (Fig. 5).

There is little variability in other skeletal elements, other than in the palatal shelf of the premaxilla which is much more extensive in its articulation with the palatal shelf of the maxilla.

Advertisement call

Males call from the ground surface beneath dense vegetation, and from prepared breeding chambers within cushions of sphagnum or edaphic lichen. Male advertisement calls are heard in loud chorus, diurnally, in spring and early summer.

The following description of the advertisement call (Fig. 7) is based on the sequence recorded by G. F. Watson. The call is a single quasi-periodic pulse train with a duration of 1009–1281 ms (mean = 1157), and consists of a series of 7–8 (mean = 7.5) short pulses (duration; range = 7.2–10.4 ms; mean = 8.74 ms) with rise times (attack) of about 1.0–3.5 ms and fall times (decay) of about 4.9–5.9 ms. The pulse rates range from 5.3 to 6.1 pulses/s (mean = 5.74) (Table 1). The calls are repeated at a rate of 2.65 calls/min. Although there is a wide spread of spectral energy (as a consequence of the short rise-times of the pulses), there are two dominant frequencies of equal energy at 2100–2140 and 2680 Hz in three of the calls, there is only one peak at 2140 Hz in two calls, and in the remaining call there are two peaks at 2120 and 2740 Hz (with the latter being lower by 2 dB).

The values obtained from each of the 18 calls recorded by P. B. Brown are presented in the recording sequence in Table 2. From an inspection of the numbers of pulses and dominant frequencies, it is suggested that calls of three or four individuals may be included in the sequence. The values for call duration, number of pulses and pulse rates, although of greater range, include those of the individual recorded by G. F. Watson. The dominant frequencies, where measured, however, are lower, ranging from 1540 to 1960 Hz.

Calling period

The calling period in alpine habitat is seasonal. Calls in chorus were heard at the type locality from early October to late December. Earliest calling heard was in the Hartz Mts on 1.x.1993, and the latest at Mt Norold (146°15'40"E, 43°15'30"S), on 2.iii.1994. Chorusing occurred in rain and whilst snow fell.

In early spring, calling was interrupted frequently by heavy snow falls, and recommenced when thaw set in. During summer, calls ceased during the warmest part of the day at temperatures above 15°C and as the

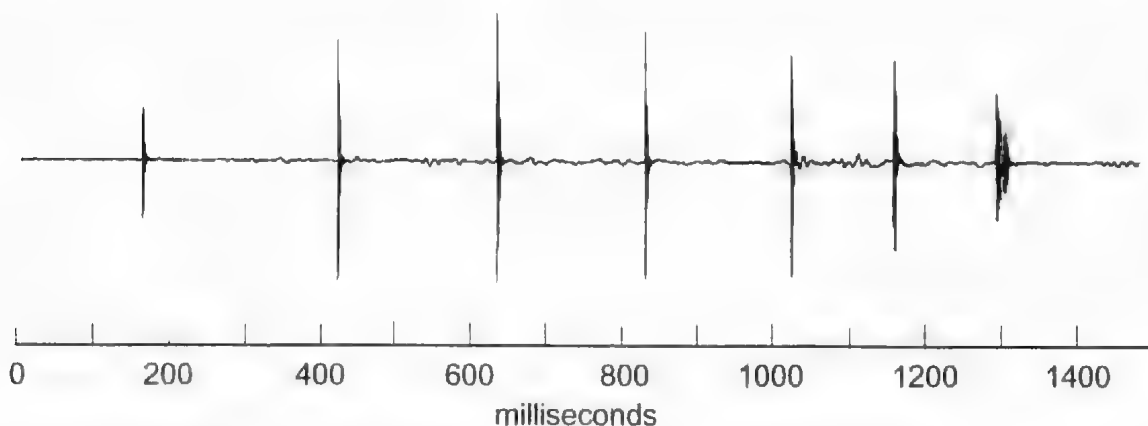


Fig. 7. A wave form display of an advertisement call of a male of *Bryobatrachus nimbus*, gen. et sp. nov. recorded at a wet bulb air temperature of 8.5°C, in the Hartz Mountains. The depicted call is the first of the series recorded by G. F. Watson. (See Table 1 for more information.)

TABLE 1. Values for six advertisement calls of a male of *Bryobatrachus nimbus* gen. et sp. nov. at the type locality at a wet-bulb air temperature of 8.5°C on 5.xii.1992.

Duration (ms)	Pulses	Pulse rate (pulses/s)	Pulse duration (ms)	Dominant frequencies (Hz)		Difference (dB)
				lower (DF1)	higher (DF2)	DF1-DF2
1148	7	5.33	9.47	2140	2660	0
1063	7	5.76	10.35	2100	2680	0
1262	8	5.67	8.59	2140	none	—
1281	8	5.56	8.40	2120	2740	2
1178	8	6.06	8.40	2140	none	—
1009	7	6.08	7.23	2140	2680	0

TABLE 2. Values for 18 advertisement calls of several males of *Bryobatrachus nimbus* gen. et sp. nov. recorded by P. B. Brown at the type locality on 30.xi.1992.

Call (ms)	Duration	Pulses	Pulse rate (pulses/s)	Dominant frequency (Hz)
1	1681	8	4.20	—
2	925	7	6.58	1740
3	1869	10	4.87	1720
4	2069	10	4.39	1540**
5	1919	10	4.74	1540**
6	2037	10	4.46	—
7	1756	10	5.20	—
8	1356	7	4.46	1800
9	634	5	6.53	1800
10	1169	7	5.19	1960*
11	698	5	5.93	1800
12	884	4	3.44	1800
13	2225	10	4.09	1620
14	2256	11	4.47	1620
15	2144	10	4.24	1600
16	2100	10	4.33	1600
17	1712	10	5.34	1800
18	2394	11	4.21	1600

* midpoint of band; ** second peak at 1820 Hz.

vegetation dried out. Individuals called in cool conditions during the early morning and in the evening (19:00–21:00) at Mt La Perouse on 1.ii.1994 (S. Corbett pers. comm.). Frogs were not heard at night.

Ziegeler (1994) observed calling in air temperatures of 4.5–12°C and relative humidities of 62–94%. The frequency of calls heard increased when there was precipitation.

Behaviour

The species is cryptozoic, and was collected during spring and summer. Calling males were collected from the surface of the peat beneath coarse, low vegetation, from within breeding chambers or nests, in cushions of sphagnum or other similar plants, beneath rocks (Ziegeler 1994), or under branches lying on or amongst vegetation. Females were found in breeding chambers with a male or, when males were chorusing in spring, on the surface of the vegetation. Males continued to call even when females occupied the same chamber.

At the type locality where a large population exists, individual frogs are regularly spaced, remaining hidden. They appear not to aggregate or to use open

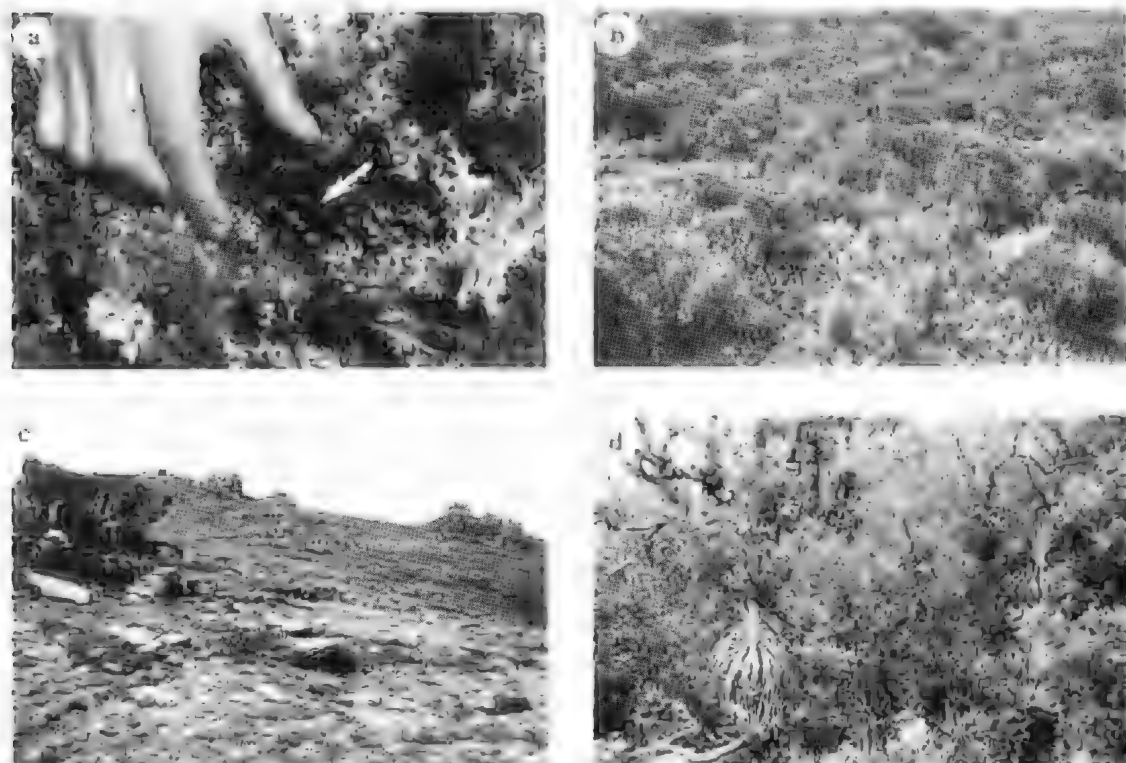


Fig. 8. A, Nest of *Bryobatrachus nimbus* gen. et sp. nov.; B, subalpine moorland habitat at Hartz Mts; type locality in middle distance viewed from the track (Photo. J. E. & A. Wapstra); C, subalpine moorland habitat at 800–1000 m altitude at Mt Hesperus; D, Implicate rainforest habitat at over 750 m altitude at Mt Bobs.

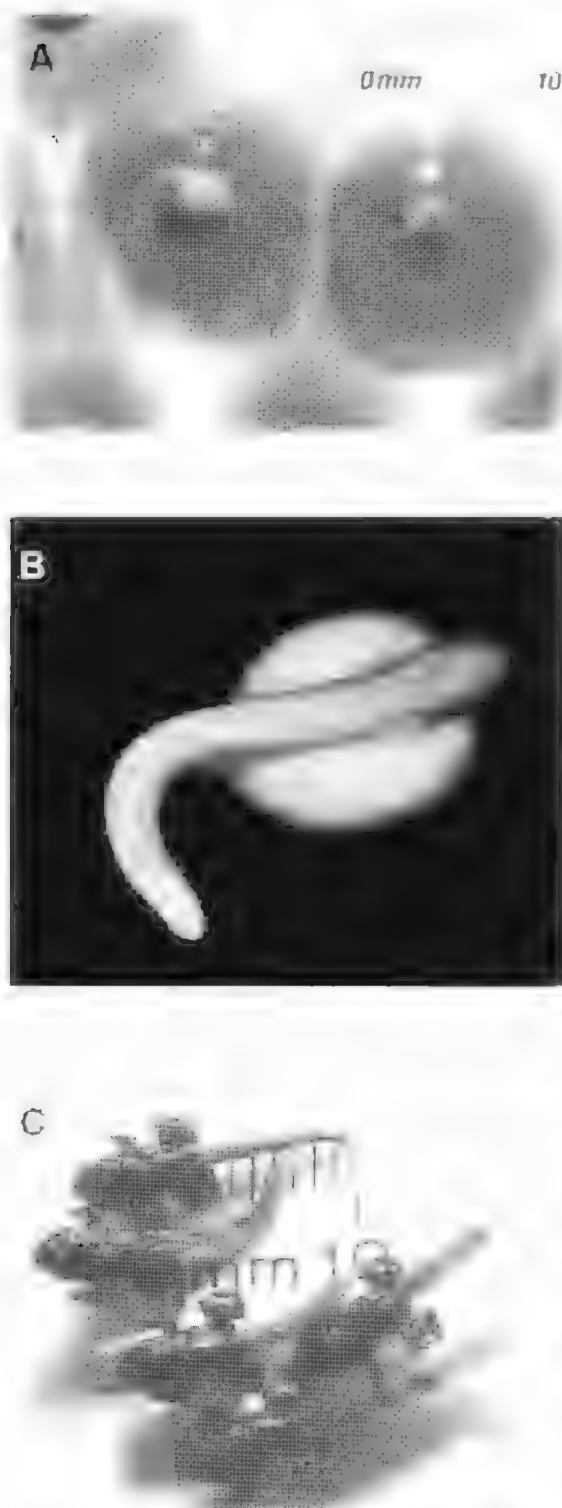


Fig. 9. *Brevibatrachus nimbos* gen. et sp. nov.: A, dorsal view of eggs; B, dorsal view of embryo at stage 5 (Townsend & Stewart 1985); C, dorsal views of froglets

surface water. None was collected during autumn or winter.

Locomotion is by crawling or walking. In the open, frogs usually crouched and remained still until disturbed and then sought cover. They jumped or swam only when forced. In captivity, both sexes displayed thigmotaxis by forming individual cavities in which to shelter in loose sphagnum. They entered the sphagnum backwards.

Development

The species breeds in spring, laying eggs in nests in moss or lichen. Nests are concealed spherical cavities (3.5–4.0 cm in diameter) in clumps of moss approximately 2–5 cm below the surface (Fig. 8A). They can be exposed by parting the stems of moss. Single males, male–female pairs (sometimes in amplexus), eggs, or froglets were found in ten nests in a small area of the type locality on three visits (24.xii.1993, 11.i.1994 and 28.i.1994). On the first visit, five nests were found. One contained 6–10 eggs, another contained five froglets (Fig. 9C), the third held a single male frog, and the remaining two nests each held a male–female pair of adult frogs (one pair included a gravid female and a male in amplexus). On the second visit three nests containing eggs were found. Two contained 12 and 14 eggs. Those in the remaining nest could not be readily counted as the jelly surrounding them had begun to merge. The last visit produced two new nests, one containing 9 eggs, and another containing 5–6 froglets. Each nest was found in a separate cushion of moss. Other empty and possibly disused nests were found in adjacent patches of moss in the same area.

Eggs containing embryos (Fig. 9B) at stage 5 of Townsend & Stewart (1985) were located on 10.xii.93 but not in nests. Two groups of eggs were found on the surface of the vegetation and contained three and six eggs respectively. The latter included four dead embryos infected with fungus.

The mean diameter of four of the newly laid eggs found on 11.i.94 was 3.49 mm (3.33–3.65), and the mean capsule diameter was 13.57 mm (13.02–14.13). They were surrounded by a single jelly membrane (Fig. 9A). These eggs cannot be ascribed to a stage as for the direct developing *Eleutherodactylus coqui* (Townsend & Stewart 1985).

The mean S–V length of five metamorphs was 6.0 mm (5.4–6.35) and the mean total length, 14.51 mm (13.97–19.05). Tail length varied considerably (Fig. 9C). Tail muscle is well developed and, tail fins narrow, equal in width dorsally and ventrally. Tail fins do not appear to be vascularised. The body is heavily pigmented; that on tail muscle being finer and that on tail fins patchy. In life the body and tail are covered with fine white dots. There is no cloacal tail piece. The mouth extends beyond the eye and the fingers and toes appear to be fringed.

Habitat

Bryobatrachus nimbus is found in subalpine moorland (Fig. 8C) and implicate rainforest in southern Tasmania (Fig. 8D). It is restricted to poorly-drained sites from lowland to subalpine localities (Ziegeler 1994). The soil type is peat overlying sandy or stony substrate (Ziegeler 1994). It occurs on Pre-Cambrian metamorphics, Upper Carboniferous-Permian sedimentary deposits, Triassic sandstone and Pleistocene-glacial deposits.

The subalpine moorland comprises a diverse range of plant communities. Five recorded communities are *Epacris serpillifolia*-*Empodisma minus*-*Gleichenia alpina* fernland, *Lepidospermum nitidum*-*Gahnia grandis*-*E. minus* tall shrubland (both occur at Hartz Mts [Fig. 8B]), *E. serpillifolia*-*Richea scoparia* low shrubland with *Astelia alpina*, *G. alpina* and *E. minus* (Adamsons Peak [146°49'E, 43°21'S]), *E. serpillifolia*-*Melaleuca squamea* open heath (Mt Sprent) and *Carpha alpina*-*Isophysis tasmanica* herbfield (Mt Sprent, Mt Hesperus [146°14'E, 43°07'20"S] [Fig. 8C]) (Ziegeler 1994).

The implicate rainforest communities are floristically complex. The shrub layers are dense and species diverse at all altitudes. At higher altitudes the dominant trees are *Nothofagus cunninghamii*, *Eucryphia milligani*, *Athrotaxis selaginoides*, *Nothofagus gunni* and *Phyllocladus aspleniifolius* and the ground cover is dense moss and/or *Astelia alpina* (Fig. 8D; 750 m, Mt Bobs [146°36'E, 43°18'S]). At low altitudes *N. cunninghamii*, *Melaleuca squarrosa* and *P. aspleniifolius* are dominant and ground cover is dense moss and *Blechnum wattsii* (Alexander Creek [146°05'E, 43°26'S]) (Ziegeler 1994).

The climate is in the perhumid cool zone of Gentili (1972) but is cool and consistently wet. The mean annual precipitation is 2500 mm in large parts of this region and is received as rain, snow, hail, fog, mist and frost evenly distributed across the seasons (Bureau of Meteorology 1991).

Distribution and abundance

Bryobatrachus nimbus occurs in mountains in southern Tasmania south of 42°48' latitude (Fig. 10). It is known from 15 localities, mostly described by Ziegeler (1994), that range from sea level to 1100 m in an area approximately 80 km × 50 km. The localities are bounded by Mt Sprent in the north-west, Hartz Mts in the north-east, Mt La Perouse in the south-east and Bathurst Harbour area in the south-west (Fig. 10). All localities are south of the Huon River and Serpentine River and none is over 40 km from the sea. At the northern and eastern edges of this distribution, *B. nimbus* is confined to sites above 800 m altitude whilst in the south-west, its range descends to near sea level.

Hundreds of males were heard in chorus at the type locality during spring 1992. Other large populations occur at known locations (Ziegeler 1994). Although geographically restricted, the species is abundant within available habitat, and calling males were estimated to occur at densities of 0.1-1.0/m².

Searches conducted further north at Philips Peak, Tyndall Range, Mt Field, Mt Anne, Mt Weld and Mt Picton failed to locate the species despite the presence of suitable habitat and weather conditions (Ziegeler 1994).

Conservation status

The species is secure. All locations where it has been recorded are in reserves, as is most of the suitable known habitat. Its habitat shows evidence of no fire or only very low frequencies of fire.

Etymology

From the Latin *nimbus* (= rain cloud), with reference to the habitat of the species.

Common name

The name "moss froglet" has been coined and used for this species (Ziegeler 1994).

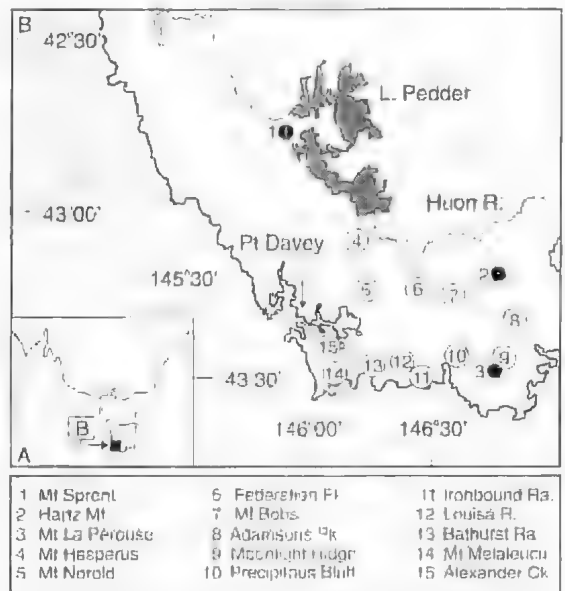


Fig. 10. Distribution of *Bryobatrachus nimbus* gen. et sp. nov. in southern Tasmania. A, Southeastern Australia, and B, localised distribution in Tasmania. Closed circles are localities from which specimens have been collected; open (numbered) circles are call records.

Comparison with other species

Bryobatrachus nimbus is distinguished from other myobatrachine frogs in Tasmania in the following ways. The species is not associated with bodies of open surface water. It is most likely to be confused with sympatric *Ranidella tasmaniensis* from which it can be distinguished by relatively short, unfringed toes and by the lack of brilliant carmine patches usually present on the flanks and the concealed surface of the thighs. The call of *R. tasmaniensis* is a quavering "bleat", slowly and irregularly repeated (Littlejohn 1970) and its microhabitat includes vegetation on the margins of open and running water. *R. signifera* has relatively long, fringed toes and is found in the vegetation on the margins of permanent or temporary water bodies. The call is a series of short rapidly-repeated notes: "crick crick crick crick" (Martin & Littlejohn 1982). *Gerrhonotus laevis* has a rounded snout with a smooth ventral skin which is usually boldly marbled with dark brown markings. The species is found in dry sclerophyll (open) forests at low altitudes (Martin & Littlejohn 1982). These authors describe the call as a harsh grating "cr-a-a-a-ack cr-a-a-a-ack, crack, crack, crack". The other myobatrachine species in Tasmania is *Pseudophryne semimarmorata* which has a smooth ventral surface strongly marbled in black and white. The head is rounded and the undersurface of the thighs are bright yellowish orange to orange in life; the call is a short, harsh "crick" repeated slowly and irregularly (Martin & Littlejohn 1982).

Comparative material examined

Arenophryne roundi: UAZ B531, B541, B762, A579-81, A760-1. *Assa darlingtoni*: UAZ A133. *Crinia georgiana*: UAZ B754, A13406. *Gerrhonotus laevis*: SAM R4260B, R8982A-E. *G. leali*: SAM R5787A. *G. victoriana*: SAM R9425 (2). *Myobatrachus gouldii*: UAZ B491, B534-5, B757, A759. *Paracrinia huxwelli*: UAZ B750. *Ranidella bilineata*: UAZ B1927, B1935. *R. deserticola*: UAZ B1930-31. *R. glauerti*: UAZ A191. *R. insignifera*: UAZ A192, A195, B929. *R. parvinsignifera*: UAZ A185, B1932-33. *R. remota*: UAZ B1928-9. *R. riparia*: UAZ A184, A189, A198. *R. signifera*: UAZ A193, A197, B898-928. *R. subvansignifera*: UAZ A190. *R. tasmaniensis*: UAZ A186. *Pseudophryne semimarmorata*: UAZ B636. *P. bibroni*: UAZ A577, A172, B532, B540. *P. cortacea*: UAZ A200, B537, B764. *P. guentheri*: UAZ A199, B539, B765. *P. occidentalis*: SAM R17522. *Tandactylus acutirostris*: UAZ B759, A205-6. *T. eungellensis*: UAZ A392. *T. theophilus*: UAZ A775-6, B752. *Uperoleia ulitissima*: SAM R40146. *U. arenicola*: SAM R17347. *U. aspera*: UAZ A872-8. *U. borealis*: UAZ A863, B862, A226. *U. capillata*: SAM R29586. *U. crassa*: UAZ A869-70, B871, B483, B486. *U. fusca*: SAM R29603, R29606-7. *U. glandulosa*: SAM R27082. *U. inornata*: UAZ A818-826, B397, B479. *U.*

laevigata: UAZ A601, B817. *U. lithomeda*: UAZ A767-8, B896, B812, A799-806. *U. littlejohni*: UAZ A1712, A1717, B1713-1716. *U. marmata*: NMV D23636. *U. micromelas*: UAZ A1722. *U. mimula*: SAM R29642-3, R29645-6. *U. myobergi*: UAZ A582, A880-9. *U. rugosa*: UAZ 1012, A1013, A816, B814. *U. talpa*: UAZ A591-4, B864. *U. trachyderma*: UAZ A621, A892-4, A595-6. *U. tyleri*: NMV D23639, SAM R29659, R29652.

Discussion

Bryobatrachus nimbus exhibits a number of unusual features in its morphology and reproductive biology. Many of the characters contributing to the recognition of the genus and species are influenced by heterochrony in other myobatrachine genera (Davies 1989). The presence of teeth on the maxillary arch; reduction of the vomers and absence of vomerine teeth; presence of a columella and reduction of the palatines, laterally, are all presumed labile features that vary intragenetically in e.g., *Uperoleia* and *Crinia* (sensu Heyer *et al.* 1982). However, none of these features either singly or in combination is definitive of *Bryobatrachus*. All are coupled with the unusual feature of fusion of the posterior portion of the vertebral column with the sacrum.

Vertebral fusions tend to be in an anterior/posterior sequence (Trueb 1973), and fusions of presacral VII and VIII with the sacrum are unusual. The nature of the fusion cannot be described as a presacral shield, as known in a few taxa including *Brachycephalus eppiphium* (Brachycephalidae), and thought to be protective on the basis of terrestriality exhibited by such taxa (Trueb 1973).

Fusions approaching that shown by *B. nimbus* have been recorded in the Bufonidae (e.g., *Didynamis*, see Grandison 1981), in *Dendrobates* (Trueb 1973), and in the Pipidae; although the fusions reported in *Pseudhymenochirus* and *Hymenochirus* by Cannatella & Trueb (1988) are inferred, and not identified by remnant vertebrae or recorded spinal foramina, vertebral fusion in *Pipa myersi* more closely approximates that in *Didynamis* (Trueb 1984). None of these families is native to Australia.

Although conforming to the myobatrachine pattern, the width of the junction of the alary processes with the hyoid plate is not as broad as in most other genera and approaches that shown by the enigmatic genus *Rheobatrachus* (Davies & Burton 1982; Mahony *et al.* 1984), the subfamilial placement of which remains contentious (Tyler 1989; Littlejohn *et al.* 1993).

Terrestrial egg deposition and direct development have evolved a number of times in Australian frogs (Martin 1967). Reproductive modes include complete intracapsular development (e.g. in the microhylids *Sphenophryne* and *Cophylax*), through hatching at

a relatively late stage in ontogeny (e.g. the myobatrachine *Pseudophryne*) to non-swimming, non-feeding larvae that are subject to bizarre forms of parental care (e.g. the myobatrachine *Axi* and the rheobatrachine *Rheobatrachus*). All of these gradations of direct development are found within the Myobatrachinae, and reproductive mode can sometimes vary intragenerically. In *Pseudophryne*, *P. douglasi* differs from congeners in laying eggs in water, and thus not relying upon flooding of nests to initiate hatching of larvae at later stages (Main 1964; Bradford & Seymour 1985), whilst in *Gerrhonotus*, *G. rosea* and *G. lutea* do not have free-swimming larval stages (Main *et al.* 1959; Main 1963).

Intracapsular development is known for the monotypic genera *Myobatrachus* and *Arenophryne* (Roberts 1981, 1984), and is inferred for *Metacrinia* (Main *et al.* 1959). The larvae of *Gerrhonotus rosea* are inactive in broken-down egg capsules which fill shallow depressions in damp soil or in the rotten centres of hollow logs (Main *et al.* 1959). Larval life of *G. lutea* resembles that of *G. rosea* (Main 1963). Such larvae are highly modified, having no mouth disc, a large yolk sac, and an elongate tail (Watson & Martin 1973). The structure of the tail reported for *G. rosea* is similar to that observed in *B. nimbus* froglets.

Although details of the life history of *B. nimbus* have not yet been described, our limited data indicate that development is intracapsular until the final stages of metamorphosis, and that the froglets stay in the nest with the broken-down egg capsules until the tail is fully resorbed and metamorphic climax is reached.

The diameters of the eggs at 3.3–3.7 mm are smaller than ovarian diameters recorded for *Arenophryne rotunda* and egg diameters in *Myobatrachus gouldii* (Roberts 1981, 1984), but within the range recorded for *Pseudophryne* spp. and for *Gerrhonotus victoriana* and *G. luewisi* (see Tyler 1989 for compilation of data). All of these species exhibit forms of direct development. Capsule diameter is particularly large, being almost double that recorded in the field for *Myobatrachus gouldii*, and 1.5 times that of eggs hydrated in the laboratory (Roberts 1981). Clutch size compares closely with those of other direct-developing species (Tyler 1989).

Four other Tasmanian species (*Ranidella signifera*, *R. tasmaniensis*, *Gerrhonotus laevis*, *Pseudophryne semimarmorata*) have advertisement calls composed of trains of pulses. The short pulse trains of *B. nimbus* are similar to those of *R. signifera*, but the call repetition rates and pulse repetition rates and dominant frequencies are higher in this latter species (Littlejohn 1964, 1970). The call of *R. tasmaniensis* is more complex, being composed of a group of pulse trains, or notes, of high and regular pulse rates (Littlejohn 1970), so that it has a bleating quality. The call of *G. luewisi* consists of a series of pulse trains in which the

pulse intervals decrease through each note (Littlejohn & Martin 1964; Harrison & Littlejohn 1985). The call of *P. semimarmorata* consists of a single complex pulse train, usually with biphasic structure (McDonnell *et al.* 1978). Hence, the advertisement call of *B. nimbus* is sufficiently unlike those of all other species of anuran occurring in Tasmania to be a reliable indicator for identification. Possibly, the most similar advertisement call of a southern myobatrachid to that of *B. nimbus* is that of *Ranidella glauerti* of south-western Western Australia, which consists of a slow pulse train and very short pulse durations (Littlejohn 1959, 1961; M. J. Littlejohn & P. G. Littlejohn unpubl.).

Bryobatrachus nimbus is most similar in external morphology and cranial osteology to *Ranidella tasmaniensis* (Davies unpubl.), in its reproductive biology to *Gerrhonotus rosea* and *G. lutea*, and in the structure of the hyoid to *Rheobatrachus*. It is not possible, therefore, to identify the sister taxon to the genus on the basis of the phenetic comparison presented here. Such an identification must await a detailed analysis of, at least, the subfamily Myobatrachinae, incorporating all available data.

B. nimbus appears to be confined to southern Tasmania despite the presence of apparently suitable habitat in highlands beyond. It has been sought north of the Serpentine and Huon River systems without success. The distribution might be explained by the extent of Pleistocene glaciation in the central highlands of the island, and the severity of the cold, dry climate in ice-free areas (Galloway 1986) making the central highlands unsuitable for it in the past, coupled with a lack of northward dispersal since.

The region currently occupied by the species has a continually wet equable climate produced by year-round high rainfall within the perhumid cool climatic zone (Gentili 1972). All localities are less than 40 km from the sea, and are subject to coastal climatic influences, particularly increased precipitation from orographic interaction with moist prevailing west to south-west winds. The direct development of the juvenile stages requires a climate free from the extremes of desiccation. It is most unlikely that the known habitat types could support the species until a very long time after a wildfire (Brown & Podger 1982). *B. nimbus* can be regarded as belonging to fire-intolerant communities, and the occurrence of fire represents the greatest potential threat to its survival.

During the present work, several clutches of developing eggs were found on the surface of moss at Hartz Mountains. The site had been covered by a snowdrift for some time. Egg-laying beneath the snow rather than in nest could account for their location and later exposure after the thaw. The embryos would be prone to desiccation before completing their development. Alternatively, stepping on patches of moss when walking across the site could eject eggs

from nest chambers. Whichever is the case, caution is advisable when working at breeding locations.

Acknowledgments

Dr Graeme Watson recorded the call used in the analysis. Dr Dale Roberts located the first nest chamber and helped to clarify the breeding biology. Dr Roy

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THE DISTRIBUTION OF NEMATODE PARASITES WITHIN THE STOMACH OF THE WESTERN GREY KANGAROO, MACRUPUS FULIGINOSUS

BY D. PAMMENT, I. BEVERIDGE & R. B. GASSER

Summary

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The distribution of strongylid nematodes in the stomachs of ten western grey kangaroos (*Macropus fuliginosus*), from Hattah, Victoria indicated that each genus encountered, *Cloacina*, *Rugopharynx*, *Labiostrongylus*, *Popovastrongylus* and *Filarinema*, occupied a specific region within the stomach. Their distribution bore no relationship to histologically defined regions of gastric mucosa, and the pathological changes detected in the mucosa were related more closely with mucosal type than with local nematode densities. The anatomical and histological features of the stomach of *M. fuliginosus* are described.

Key Words: Nematoda, Strongyloidea, *Macropus*, Macropodidae, distribution, gastric anatomy.

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Introduction

The differential localisation of multiple, closely-related parasitic nematode species within the gastrointestinal tract of their hosts has been investigated extensively in the case of the oxyuroid parasites of tortoises (Petter 1963, 1966; Schad 1963). Niche diversification has been demonstrated on the basis of differences in the linear and radial distribution of nematode species and in their feeding behaviour. Inglis (1968) suggested that because of the complex anatomy of their stomachs and the diversity of nematode species harboured within them, the kangaroos represented an equally suitable group of hosts for studying the coexistence of congeneric and confamilial nematode species within the same host. Studies undertaken to date support Inglis' (1968) suggestion, but have been limited to the red kangaroo, *Macropus rufus* (see Mykutowycz 1964; Dudzinski & Mykutowycz 1965; Arundel *et al.* 1979) and the tammar wallaby, *Macropus eugenii* (see Smales & Mawson 1978a). In this study, the distribution of nematodes within the stomach of the western grey kangaroo, *Macropus fuliginosus*, was investigated and relationships between this distribution and gastric mucosal histology examined. Pathological changes in the gastric mucosa were also investigated. Examination of *M. fuliginosus* allowed analysis of the relationships of four confamilial genera, and in the case of one genus, *Cloacina*, the comparative distributions of several congeneric species.

Methods

Collection of material

Stomachs were obtained from ten western grey kangaroos, *Macropus fuliginosus*, culled at Hattah Lakes National Park (34°45'S, 142°15'E), Victoria in November 1990. Animals were shot, weighed and sex and body measurements were recorded. The stomach was removed rapidly from the carcass, the oesophagus

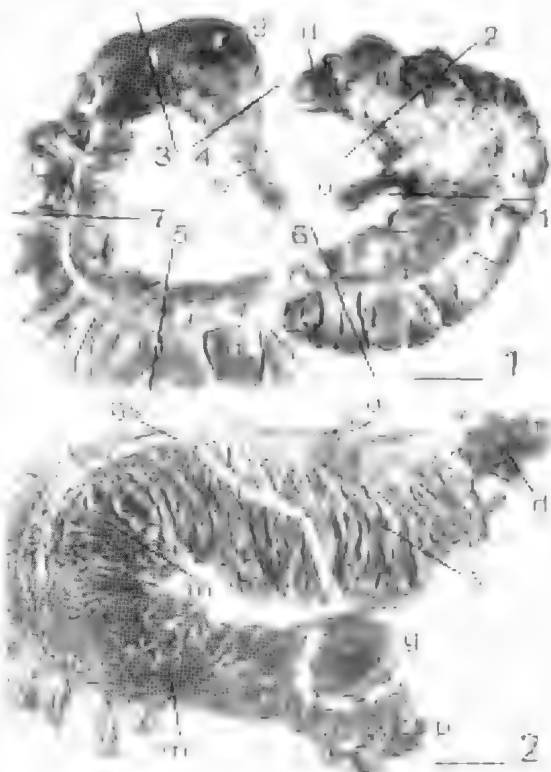


Fig. 1. Stomach of *Macropus fuliginosus*, unopened. Lines and numbers indicate the positions of ligatures and the order in which they were applied.

Anatomical landmarks shown are the oesophagus (o), the proximal diverticulum (d), the gastric pouch (g) and the pylorus (p). Scale bar: 5 cm.

Fig. 2. Stomach of *Macropus fuliginosus*, opened to show distribution of the principal types of mucosal surfaces, delineated by white broken lines: the glandular mucosa of the proximal diverticulum (d), the squamous epithelium of the saccular and tubular fore-stomach (s), proximal and distal to the oesophagus (o) and the gastric sulcus (gs), the glandular mucosa of the tubular fore-stomach (m), the mucosa of the gastric pouch (g) and pylorus (p). Scale bar: 5 cm.

and pylorus were tied with string, numerous small punctures were made in the stomach wall and the entire stomach was immersed in 50 litres of neutral buffered 15% formol saline (6% formaldehyde).

In the laboratory, stomachs were washed in water to remove formalin, photographed and weighed, then subdivided with ligatures and opened. Anatomical nomenclature for the regions of the stomach follows Hume (1982). The ligatures were placed in the following order (Fig. 1): at the level of the oesophageal opening (1), midway between the oesophageal opening and the extremity of the saccular forestomach (2) at the junction of the tubular forestomach with the gastric pouch (3) and at its junction with the pyloric antrum (4). Subsequently, the tubular forestomach was subdivided by three ligatures (5-7) placed equidistantly. The content from each section was removed and weighed. Within each section of the stomach, a transverse strip of tissue was removed, embedded in paraffin, sectioned at a thickness of 3 μ m, and stained with haematoxylin and eosin for histological examination. The extent of the different epithelial regions of the stomach was determined by cutting out the entire squamous, mucus-secreting, glandular (proximal diverticulum), gastric and pyloric regions and weighing them. The average weight per cm² of each mucosal type was determined by weighing 2 cm² portions of each mucosal type, and the area occupied in each stomach was calculated by dividing the two.

As a control for histopathological examination, a single adult *M. fuliginosus* from Healesville Sanctuary, killed for other reasons, was examined. This animal had been treated regularly with anthelmintics to remove nematodes prior to death by intravenous injection of a barbiturate. Portions of gastric mucosa were fixed immediately in 10% neutral buffered formol saline (4% formaldehyde) and were processed for histological examinations as described above.

Parasitological observations

The total number of nematodes in each section of the ten stomachs was estimated by a dilution technique

(Clark *et al.* 1971) and the number of each species present determined by clearing all nematodes in the appropriate subsample in lactophenol and identifying them to species under a compound microscope.

To establish whether or not parasite distribution was affected by this method of fixation, two additional stomachs collected were ligated with string at six points along their length before being immersed in formaldehyde solution.

Representative specimens of each nematode species have been deposited in the South Australian Museum (SAM), Adelaide. Nomenclature of species of the genera *Labiostrongylus* and *Cloacina* is currently under revision. For this study, the species names applied are the same as those used by Beveridge & Arundel (1979).

Results

Gross anatomy of the stomach

The gross anatomy of the stomach of *M. fuliginosus* (Figs 1, 2) resembles that of *M. giganteus* (Langer *et al.* 1980; Dellow 1982). Wet weight of stomach contents (Table 1) in individual sections demonstrated that sections 1 and 2 (= the saccular forestomach (Langer *et al.* 1980)) constituted 22.3% of total stomach weight, sections 3-6 constituted 73.5% of total stomach weight (= tubular forestomach), and sections 7 and 8 constituted 4.3% of total stomach weight (= hind stomach). The gastric sulcus was prominent and extended halfway along the tubular forestomach.

Relative surface areas occupied by different epithelial types (Table 2) demonstrated that squamous and mucus-secreting epithelia were the two predominant types. The proximal diverticulum of the saccular forestomach was lined by a distinctive, glandular epithelium. The remainder of section 1 and section 2 of the stomach is lined by squamous epithelium. Apart from the gastric sulcus which is covered with a squamous epithelium, sections 3 to 6 are lined with cardiac epithelium. Section 7 has an acid-secreting fundic epithelium, while section 8 is lined by a distinctive pyloric epithelium.

TABLE 1. Wet weights of content of eight different regions of the stomach of ten *Macropus fuliginosus* from Hattah Lakes National Park, Victoria.

Stomach Section No.	Mean weight (g)	Range (g)	Standard Deviation	Proportion of Total Weight (%)	Predominant Epithelial Type
1*	89	46-151	32	4.2	s (squamous)
2	387	55-638	322	18.1	s
3	348	109-548	134	16.3	m (mucous)
4	465	145-1203	299	21.8	m
5	428	128-834	235	20.0	m
6	329	71-774	292	15.4	m
7	78	8-169	50	3.7	g (gastric)
8	12	0-35	12	0.6	p (pyloric)
Total	2136	712-4670	—	100	

* For key to stomach sections, see Fig. 1.

TABLE 2. Area, as a percentage of the total, occupied by different epithelial surfaces in the stomach of ten *Macropus foliginosus* from Hattah Lakes National Park, Victoria.

Epithelial Type	Percentage of Total Stomach Area Occupied	Standard Deviation
Squamous	31	11
Mucus secreting (tubular forestomach)	53	10
Glandular (anterior gastric diverticulum)	5	1
Gastric	5	3
Pyloric	5	1

Histological features of gastric epithelia

Squamous epithelium

This epithelium ranged from 80–320 μm in thickness. Basal cells in this region were irregularly cuboidal in shape, nuclei were relatively small, basophilic and had a prominent dark nucleolus. The cytoplasm was compact, eosinophilic and cell margins were indistinct. In the mid-region of the epithelium, cells were enlarged, cell margins were readily distinguishable, irregularly cuboidal or polygonal in shape with an enlarged, pale nucleus and prominent nucleolus. Margination of chromatin was evident in most nuclei. Towards the lumen of the stomach, cells became squamous and the cytoplasm more densely eosinophilic. The nuclei were indistinct. On the surface itself, flattened keratinised cells were visible sloughing into the lumen, and in several sections, a distinct layer of adherent bacteria was evident; closely applied to the superficial keratinised layer. The squamous epithelium was folded, with interdigitations of the lamina propria projecting into the base of the folds.

Cardiac epithelium

This epithelium was up to 600 μm thick and was composed of elongate, parallel glands 45 μm in width. The cells lining the glands were cuboidal to columnar, 25 μm in length and 10 μm wide. The glands consisted of two distinct cellular components. The cytoplasm of cells at the base of the glands was faintly eosinophilic and had a foamy appearance; cell boundaries were distinct. Nuclei were situated at the bases of the cells; they were slender and elongated, and usually demonstrated emargination of chromatin and a prominent, small nucleolus. Cells in the mid-region of the glands were eosinophilic and the cytoplasm had a granular appearance. Nuclei were large and rounded with a prominent nucleolus and punctate, emarginate chromatin. Surface epithelial cells were longer and

more slender than cells within the glands. The lamina propria was very narrow and was bounded internally by a broad lamina muscularis mucosae.

Epithelium of the proximal diverticulum

This epithelium of the proximal diverticulum of the saciform forestomach differed from that of the cardiac region (Fig. 3). The epithelium was extremely thick, up to 1.8 mm, and was composed of elongate glands, up to 1.55 mm long and 0.4 mm wide, which became sinuous towards the base. Cells lining the glands were cuboidal in shape, approximately 15 μm by 10 μm in size with a highly eosinophilic cytoplasm. The nuclei were small and were situated at the base of the cell with emargination of chromatin or with chromatin distributed in a punctate pattern, and a small nucleolus. The lumina of glands were dilated and contained a highly eosinophilic fluid, presumably secreted by the glands.

Fundic epithelium

This epithelium was 1.55 mm thick and was composed of parallel, elongate glands. The histological appearance of the glands was similar to that found in other mammals, with elongate surface cells, cuboidal mucous neck cells at the anterior ends of the glands, and chief cells and parietal cells towards the base.

Pyloric epithelium

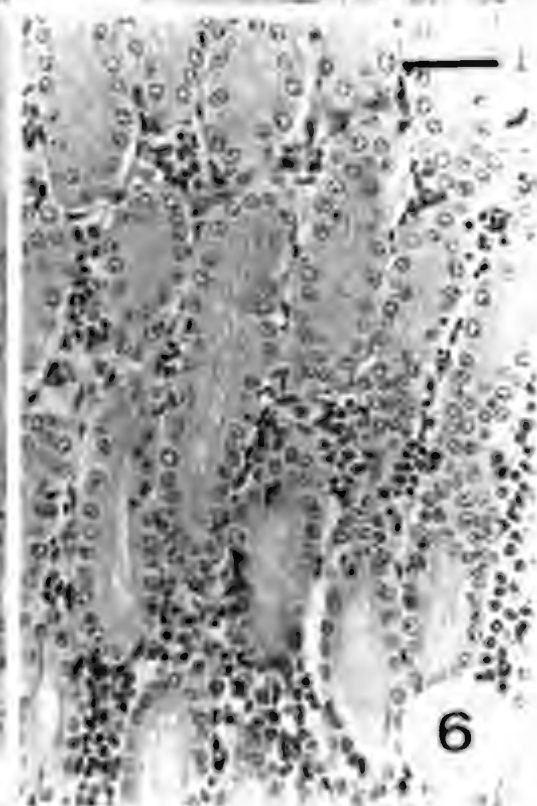
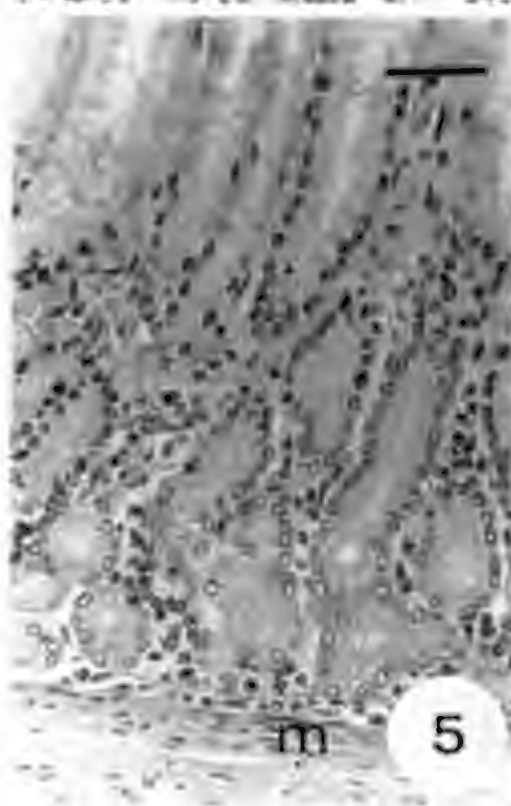
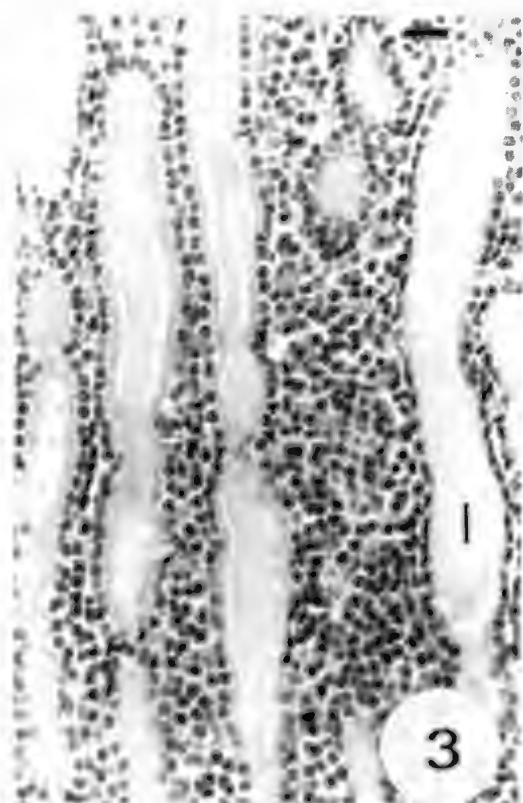
This epithelium was 1.2 mm thick and consisted of groups of very long slender glands curving inward towards the stomach lumen, with slightly sinuous bases. Cells at the basal region were cuboidal to columnar, with pale, foamy, eosinophilic cytoplasm, prominent nuclei with emargination of chromatin and a large nucleolus. In the mid-region of the glands, cells tended to be low cuboidal in shape with a more eosinophilic cytoplasm than cells at the base. The lamina propria was narrow and a prominent lamina muscularis mucosae was present immediately below the base of the glands.

Histopathological changes in the epithelia

In spite of the large numbers of nematode parasites present in the stomachs of kangaroos, no gross pathological changes were observed in the mucosa.

The squamous epithelium demonstrated few histopathological changes. Occasional small clusters of lymphocytes and macrophages were evident in the mid-region of the epithelium, or in the lamina propria (Fig. 4). Eosinophils were occasionally prominent in the lamina propria. Accumulations of inflammatory cells were visible, most frequently close to the junction of the squamous and cardiac epithelia.

The glands of the cardiac region were intact histologically and no developing nematodes were seen within glands. The lamina propria, however, was diffusely



infiltrated with mononuclear cells and granulocytes, principally eosinophils, with occasional large, focal accumulations of cells (Figs 5, 6). The submucosa was also uniformly infiltrated with the same inflammatory cells.

The proximal diverticulum invariably exhibited prominent infiltrations of the lamina propria with mononuclear cells, predominantly plasma cells, and lymphocytes, with a few eosinophils, sometimes to the extent that inflammatory cell accumulations obliterated individual glands (Fig. 3). In spite of the sometimes intense but chronic inflammatory reaction, very few nematodes were seen within glands. Those encountered were within or just below the epithelium and were surrounded by large accumulations of inflammatory cells. The fundic mucosa exhibited no significant pathological changes. The pyloric mucosa was histologically normal in most animals, but in several kangaroos, the megalo-schizonts of a coccidium developing towards the base of the glands obliterated numerous glands in the vicinity. As common as the schizonts were areas of necrosis and inflammatory cell debris indicating a site where a schizont had ruptured to release merozoites. An intense inflammatory reaction surrounded megalo-schizonts, characterised by large numbers of neutrophils and eosinophils.

Numbers and distribution of nematodes

The numbers of nematode parasites found in each of the 10 kangaroos examined are shown in Table 3.

The distribution of nematode species and genera in terms of absolute numbers in each section are shown in Figs 7-8. Expressing the results as densities (worms per g of stomach content) produced similar results, with the sole exception of section 1 of the stomach, in which densities of *Cloucinia* spp. were higher than in other sections. Distributions of the genera differed. *Cloucinia* spp. occupied the anterior sections (1-4) of the stomach, *Labiostromylus kungi* and *L. cf. bipapillosus* (sensu Beveridge & Arundel 1979) occupied a relatively restricted region in the third segment, and *R. australis* and *P. pearsoni* occurred in sections 3-6 of the tubular forestomach. Very few nematodes were detected in regions 5-6 of the tubular forestomachs. In the gastric pouch (section 7), the only nematode species encountered was *Filurnema australis*. This is a new host record. *F. australis* was found in two animals, with two nematodes in each animal. No nematodes were found in section 8. Comparison of data from these 10 kangaroos with those from the two animals whose stomachs had been ligated prior to fixation revealed no differences in the distribution of parasites within the stomach.

TABLE 3. Numbers of helminth parasites in the stomachs of ten *Macropus fuliginosus* from Hutchie Lakes National Park, Victoria

Kangaroo No.	<i>Cloucinia</i> spp.	<i>Labiostromylus</i> spp.	<i>Ragopharynx australis</i>	<i>Peponostromylus pearsoni</i>
1	480	15	37,990	0
2	3,300	560	73,000	1,060
3	1,400	15	80,870	5,380
4	1,310	50	15,850	25
5	2,200	0	184,100	2,500
6	100	40	1,360	20
7	2,200	25	66,840	1,400
8	8,300	50	121,100	4,000
9	270	400	170,600	1,500
10	1,580	25	81,590	125
Mean	2,115	120	83,330	1,600
Standard Error of Mean	755	62	19,125	586

Figs 3-6. Histopathological changes in different regions of the stomach of *Macropus fuliginosus* associated with nematode parasitism. 3, glandular epithelium of the parietal diverticulum showing dilated lumina (1), filled with eosinophilic secretion, and massive infiltrations of lymphocytes and plasma cells between glands; 4, squamous epithelium (s) of the saecular forestomach with minimal inflammatory change; 5, base of glands of cardiac mucosa from tubular forestomach showing diffuse infiltration of lamina propria with mononuclear cells (m, muscularis mucosae); 6, distal region of glands of cardiac mucosa showing diffuse infiltration of lamina propria with mononuclear cells. Scale bars: Fig. 3, 10 μ m; Fig. 4, 100 μ m; Figs 5, 6, 50 μ m.

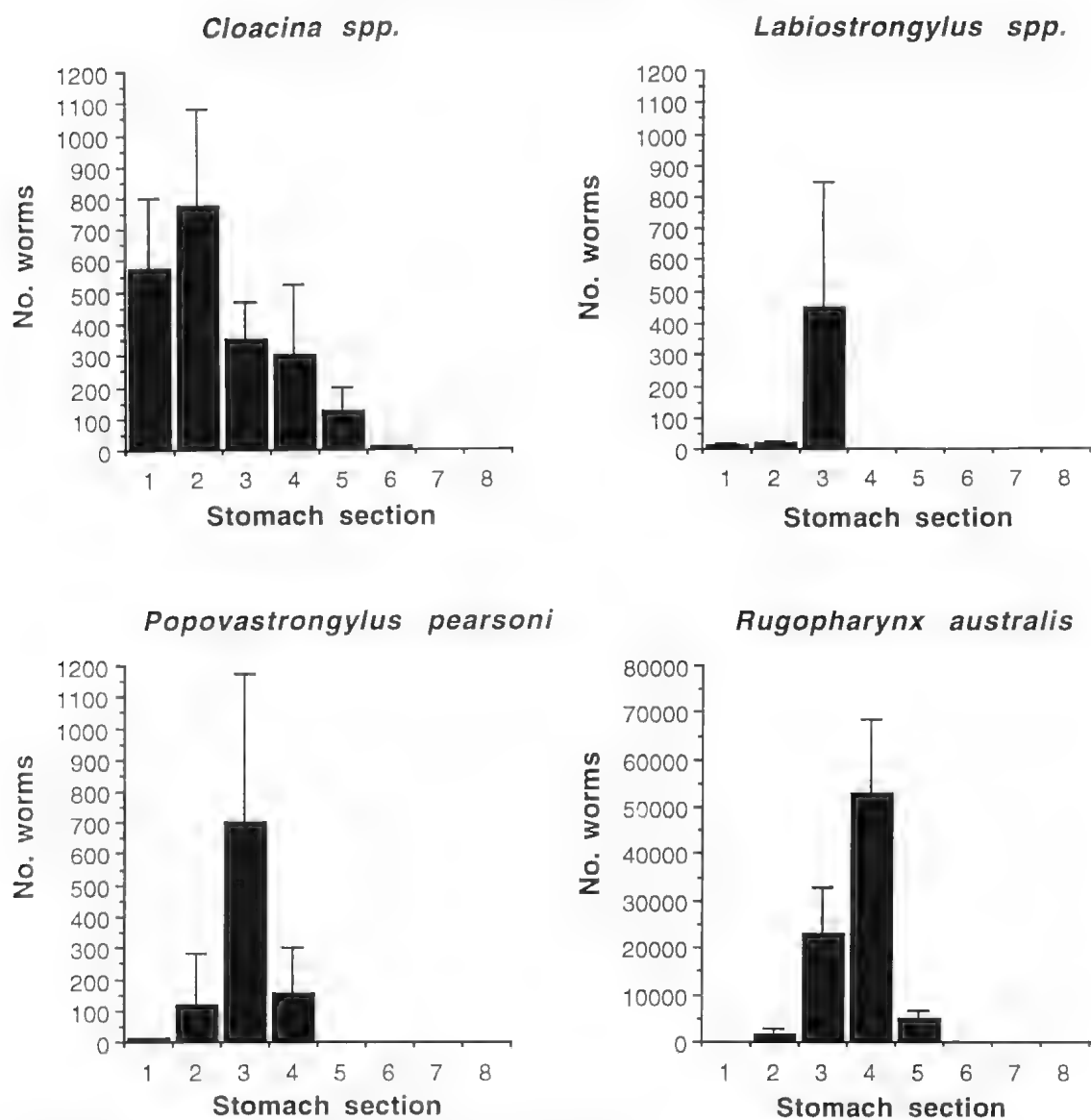


Fig. 7. Distribution of genera of strongyloid nematodes in eight regions of the stomachs of ten *Macropus fuliginosus* from Hattah, Victoria. (Bars represent standard errors of means.)

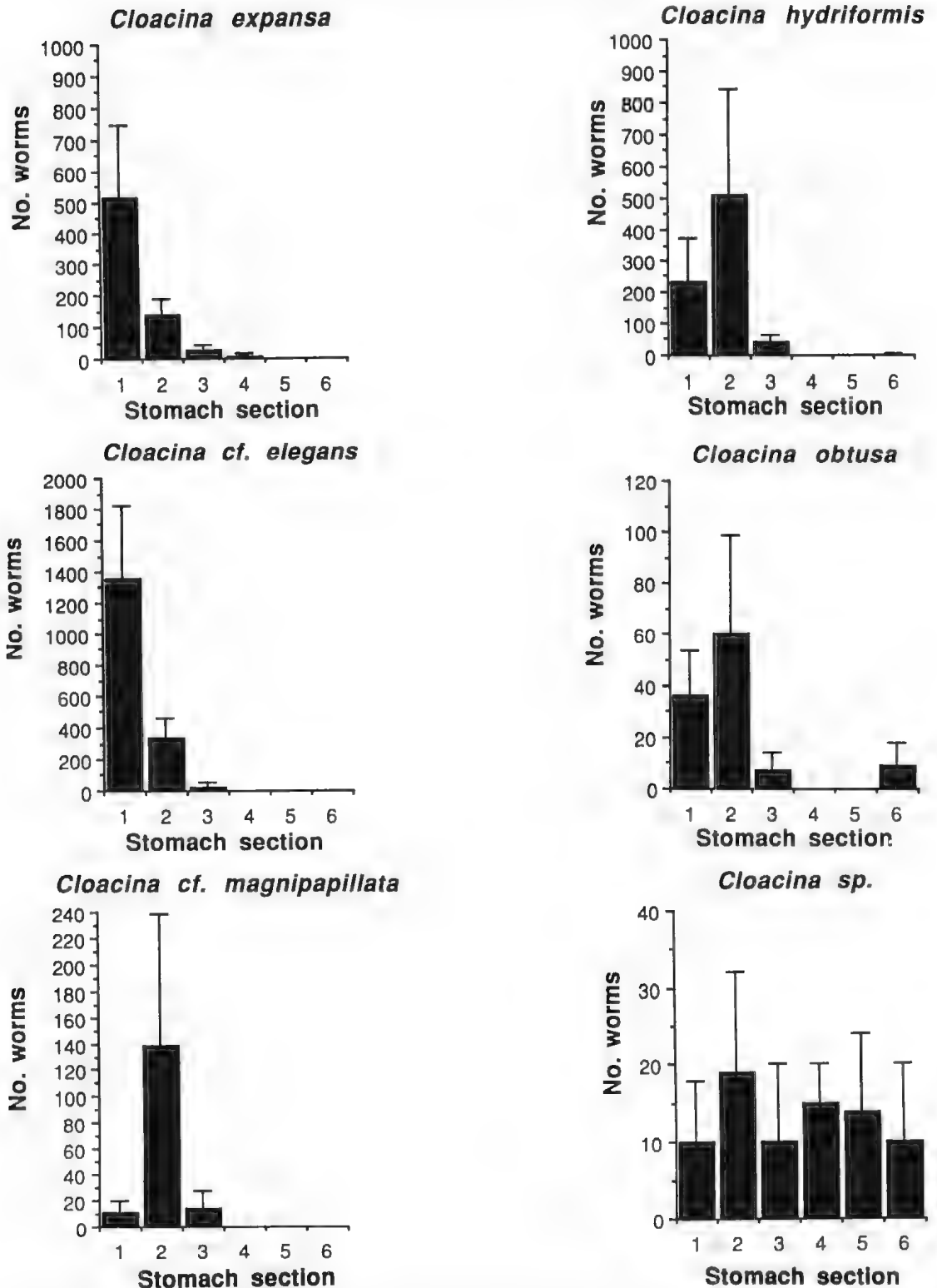


Fig. 8. Distribution of species of *Cloacina* in the eight divisions of the stomach of ten *Macropus fuliginosus* from Hattah, Victoria. (Bars represent standard errors of means.)

Discussion

The gastric anatomy of macropodids was reviewed by Hume (1982). The anatomy and histology of the stomach of the eastern grey kangaroo, *M. giganteus*, has been described previously (Schaler & Williams 1876; Langer *et al.* 1980; Dellow & Hume 1982). However there is no comparable information for the closely related species *M. fuliginosus*. In addition, while the histological and ultrastructural features of the stomach of the tammar wallaby, *Macropus eugenii*, have been described in detail (Gemmill & Engelhardt 1977), data for the eastern grey kangaroo are much more limited. We examined pathological changes in the mucosa associated with nematode parasitism and the distribution of nematodes in relationship to epithelial types and therefore an examination of both the gross and microscopic features of the stomach of *M. fuliginosus* was necessary. In this study, the gross anatomy of the stomach of *M. fuliginosus* did not differ significantly from that of *M. giganteus*. Proportions by weight of the three principal stomach regions in *M. fuliginosus*, saccular forestomach, tubular forestomach and hind stomach (22%, 74% and 4%), resembled that of *M. giganteus* closely (23%, 70% and 7%). The histological results from this study provide additional information on gastric anatomy of grey kangaroos. The most significant difference from earlier works is the recognition that the mucosa of the proximal diverticulum of *M. fuliginosus* is distinctly different histologically from that of the cardiac region and consists of elongate parallel glands producing an eosinophilic secretion. The same is true for *M. giganteus*, although the histological differences have not been reported in the literature, and both stomach regions have been considered to have an identical mucosal type (Hume 1982), a conclusion which would appear to be erroneous. Although anatomically distinctive, the function of this isolated area of glandular mucosa is unclear.

Anatomical terms applied to the stomachs of kangaroos are not consistent (see Hume 1982). The system of nomenclature suggested by Richardson (1980) as conforming most closely to *Nomina Anatomica Veterinaria* is suitable for descriptive purposes, but is not well suited to functional studies. The terminology used by Hume (1982) in which the stomach is divided into saccular forestomach, tubular forestomach and hindstomach is more appropriate when dealing with the distribution of nematodes and of epithelial types and has therefore been utilised in this study.

Determining the position of nematodes within an organ clearly requires very rapid fixation or immobilisation of the nematodes following the death of the host. With small host species, this has been achieved using rapid freezing (Schad 1963; Bush & Holmes 1986) or rapid immersion in fixative (Rohde

1980). With large hosts such as kangaroos, the technical difficulties are greater. The methods used in the past have been ligation of the stomach immediately following the death of the host in the laboratory (Smales & Mawson 1978b) or ligation following host death in the field (Dudzinski & Mykutowycz 1965; Arundel *et al.* 1979). Difficulties occur in accurately identifying anatomical "landmarks" and placing ligatures on stomachs under field conditions and therefore the approach taken here was to rapidly immerse the entire stomach in a large volume of formaldehyde solution and carry out its subdivision in the laboratory. That this did produce an accurate representation of the longitudinal distribution of nematodes was confirmed by comparison with data from the stomachs of two kangaroos which were ligated in the field prior to fixation.

In spite of technical limitations, each of the nematode genera exhibited a restricted localisation within the stomach. Data have been presented (Fig. 7) as absolute numbers of worms in each stomach section rather than number of worms per gram of stomach content (density). The only genus for which the distribution pattern is altered in comparing density rather than absolute numbers is *Cloucina* because of the high density of nematodes in section 1 of the stomach. *Cloucina* spp. were located primarily in the saccular forestomach with maximum densities in Section 1. *Labiostrongylus* spp. were also present in the saccular forestomach, but maximum numbers occurred in section 3 at the anterior end of the tubular forestomach. Both *Rugopharynx australis* and *Popovastrongylus pedryoni* occurred principally in the tubular forestomach and all strongyloid nematodes were absent from the hindstomach (sections 7-8), an area of the stomach characterised in macropodids by a low pH (Dudzinski & Mykutowycz 1965; Smales and Mawson 1978b), and inhabited only by the trichostrongyloid genus *Filarinema*.

The distribution of nematodes within the stomach of *M. fuliginosus* is similar to that reported for other kangaroo species. Smales & Mawson (1978b) found that *Cloucina* spp. were most abundant in the saccular forestomach of *M. eugenii* while *R. australis* was most abundant in the tubular forestomach. Likewise, Arundel *et al.* (1979) found that maximum numbers of *R. australis* occurred in the tubular forestomach of *M. rufus*. The distribution of *Labiostrongylus* spp. was restricted in *M. fuliginosus* (mainly in section 3) when compared with data from other hosts (Dudzinski & Mykutowycz 1965; Smales & Mawson 1978b) but this may be related to parasite density. The number of *Labiostrongylus* spp. in the present study was low (mean = 120, Table 3). Dudzinski & Mykutowycz (1965) divided their specimens of *M. rufus* infected with *L. longispicularis* into "heavily infected" (>200 worms) and "lightly infected" (<200 worms) hosts.

They showed that the maximum number of *L. longisplachis* always occurred in the tubular forestomach but that with increasing abundance, the numbers of nematodes in the saecular forestomach rose. If similar mechanisms operated in *M. fuliginosus*, then higher parasite densities would be expected in result in a significant increase in parasite numbers in sections 1 and 2 of the stomach. *P. pearsoni* in our study occurred predominantly in the tubiform forestomach (sections 4 and 5) but in *M. eugenii*, the same species occurs primarily in the saeciform forestomach (Smales & Mawson 1978b). The reasons for this difference are not known, but it may reflect differences in the anatomy and physiology of the stomachs of the grey kangaroos (*M. giganteus* and *M. fuliginosus*) when compared with that of *M. eugenii* (see Richardson 1980; Langer *et al.* 1980; Dellow 1982; Dellow & Hume 1982) or may be a function of host associations. *P. pearsoni* is a common and abundant parasite in *M. eugenii* (see Smales & Mawson 1978a). Its distribution in *M. fuliginosus* is much more restricted, being known only from Kangaroo Island, South Australia (Beveridge 1986), Kersebrook, South Australia (Wiesner, unpublished¹) and Hattah, Victoria. It was not encountered in a survey of the parasites of 40 *M. fuliginosus* by Beveridge & Arundel (1979). *M. fuliginosus* may be an abnormal or unusual host for the parasite and this may be reflected in a differing distribution of the nematode in the stomach.

The distribution of congeneric parasite species was not investigated in the case of the two species of *Labiostomylus* because of their relatively restricted distribution within the stomach. Of the several species of *Clouaina* present, only three, *C. expansa*, *C. hyaliformis* and *C. cf. elegans* occurred at sufficiently high densities to permit comparisons. In each case, there was no evidence of differing distributions. Each parasite had a maximum density in the blind sac of the saecular forestomach. One *Clouaina* species occurred in sections 1 to 6 of the stomach, but in very low numbers only. The data therefore suggest that there is no or very little regional separation within the stomach when several congeneric species are present.

The lack of differences in the distribution of congeneric species of *Clouaina* contrasts with studies on the oxyurid nematodes of tortoises (Schad 1963; Petter 1966) in which each nematode species was shown to have a restricted niche. The results obtained here, with no apparent niche segregation, are consistent with the hypotheses proposed by Rohde (1980) for monogenean parasites of fish, in which restricted

niches were absent but aggregations of conspecific parasites were assumed to occur in order to facilitate reproduction (Rohde 1977). Competition was not considered to be a significant element in distributions as niches were super-abundant and were not saturated. In the specimens of *M. fuliginosus* examined, the numbers of nematodes present per kangaroo were low when compared with previous studies (Beveridge & Arundel 1979; Wiesner, unpublished¹) in which total nematode numbers ranging from 300,000 to 500,000 were encountered in some kangaroos. These data imply that the numbers of niches available for most species of gastric nematodes in *M. fuliginosus* are large and if this is the case, competition would not be expected to be a major factor affecting nematode distributions. A far larger sample of kangaroos should be examined to test for evidence of interactions between component parasite taxa (Hoste & Cabaret 1992). However, little or no evidence of competition has been found in stomach-inhabiting nematodes in *M. rufus*, *M. giganteus* or *Petrogale* spp. (see Hoste & Beveridge 1993).

Histopathological changes in the gastric mucosa were restricted to diffuse infiltrations of mononuclear cells in the lamina propria between glands. Changes in the squamous epithelium were negligible. The mononuclear cellular infiltrations were diffuse and there was no apparent relationship with nematode distribution. Cellular changes in the lamina propria were most marked in the tubular forestomach, and it was here that the greatest numbers of nematodes were found. However, in the saecular forestomach where *Clouaina* spp. were dominant, the marked changes in the glandular epithelium compared with the lack of change in the adjacent squamous epithelium suggested that the type of epithelium present significantly influences the extent of pathological changes seen. In the fundus, an area essentially devoid of nematodes, no significant pathological changes were found.

In the pyloric antrum, focal lesions detected were caused by schizonts of a species of *Eimeria*. Although a number of species of this genus are known to occur in *M. fuliginosus* (see Barker *et al.* 1989), the species present in the pylorus could not be identified, because only the oocysts excreted in faeces have been described.

In the study of the pathological changes induced in the stomach of *M. giganteus* by nematodes, Arundel *et al.* (1990) commented on macroscopic lesions caused by *Labiostomylus* spp., by *Strongylodes* sp. and by *Rugopharynx roseumariae*. None of the lesions they reported was found in *M. fuliginosus* at Hattah, although it is evident that the presence of *Clouaina* spp. and *R. australis* in the stomach resulted in a diffuse gastritis similar to the inflammatory changes induced by strongyloid nematodes in the large intestines of equids (Barker & van Dreumel 1985).

¹ D. Wiesner, 1985. Comparison of helminth parasite burdens in western grey kangaroos, *Macropus fuliginosus* (Desmarest, 1822) grazing natural, improved and degraded pastures. Research by Agricultural College, unpublished thesis.

The mean intensity of infection of kangaroos with gastric nematodes at Hattah (Table 3) (mean 87,200 nematodes) was similar to that (95,200) reported from 40 free-ranging *M. fuliginosus* collected in western Victoria and in South Australia by Beveridge & Arundel (1979). Given the high density of kangaroos at Hattah at the time of the collection of 78 per square kilometre (Morgan 1990), it was considered possible that parasite abundance might also be higher, as occurs in populations of *M. giganteus* (Arundel *et al.* 1990), but this was not the case. A more detailed study of the epidemiology of nematode infections in *M. fuliginosus* in western Victoria is required before the significance of the current data can be assessed.

Acknowledgements

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GROWTH OF THE SEAGRASS POSIDONIA SINUOSA CAMBRIDGE ET KUO AT LOCATIONS NEAR TO, AND REMOTE FROM, A POWER STATION THERMAL OUTFALL IN NORTHERN SPENCER GULF, SOUTH AUSTRALIA

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The growth of the seagrass *Posidonia sinuosa* was monitored in northern Spencer Gulf, South Australia between late 1986 and 1990 at a site within the influence of the thermal discharge from the Northern Power Station, and at a Gulf ambient site. *P. sinuosa* growth was also monitored in Pt. Paterson, a large shallow bay surrounded by extensive mudflats, immediately to the south of the power station, but beyond the influence of the thermal plume.

Key Words: seagrass growth, water temperature, Spencer Gulf.

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The growth of the seagrass *Posidonia sinuosa* was monitored in northern Spencer Gulf, South Australia, between late 1986 and 1990 at a site within the influence of the thermal discharge from the Northern Power Station, and at a Gulf ambient site. *P. sinuosa* growth was also monitored in Pt Paterson, a large shallow bay surrounded by extensive mudflats, immediately to the south of the power station, but beyond the influence of the thermal plume.

P. sinuosa meadows adjacent to the power station show relatively minor reductions in growth characteristics (leaf blade biomass, productivity, and leaf growth) compared to those in Gulf ambient conditions, despite the fact that summer water temperatures adjacent to the discharges are consistently slightly higher than Gulf ambient and have reached 28°C, a temperature comparable to the highest field temperatures previously recorded for *Posidonia*.

However, in the naturally warm waters of Port Paterson, where average summer water temperatures are marginally higher than those within the influence of the thermal plume and where intermittent peak temperatures exceed 30°C, *P. sinuosa* has significantly reduced productivity, standing biomass, blade length and blade growth rate, typical of *Posidonia* species in marginal environments.

Despite the minimal effects of the current discharge on the seagrasses, the evidence from Pt Paterson suggests that in northern Spencer Gulf where summer temperatures are more typical of a subtropical than a temperate marine environment, *P. sinuosa* is near the upper limits of its temperature tolerance during the hottest time of the year. Should there be localised increases in maximum water temperatures in the Gulf from future thermal discharges (> 30°C), there is the potential for more widespread occurrence of stunted seagrasses such as found in the shallow waters of Pt Paterson. One possible consequence of this could be localised increase in the movement of sediments on the sloping banks of the Gulf channel.

KEY WORDS: seagrass growth, water temperature, Spencer Gulf

Introduction

Spencer Gulf, South Australia, extends about 200 km inland to the arid mid north of South Australia (Fig. 1). Northern Spencer Gulf is defined as that portion of the Gulf north of 33°S. The waters of the northern Gulf are characterised by high summer salinities, 48 (Nunes & Lennon 1986), and summer temperatures in the mid to high 20s°C (Ainslie *et al.* 1989).

Shepherd (1983) found that the subtidal benthic communities were "impoverished in terms of the overall species richness" and concluded that this may be indicative of a stressed hypersaline environment. He suggests that it is critical that the component parts of the biological system of the northern Gulf "should receive very detailed study to determine its capacity to receive additional stresses".

The extensive seagrass meadows are an important component of the biological system of the gulf, as a habitat and nursery region, for their intrinsic conservation value, and also for the role they play in stabilising sediments, particularly the sloping banks of the Gulf channel¹.

In 1955 a 90 Megawatt (MW) thermal power station, Playford Power Station, was established on the eastern shore of northern Spencer Gulf, south of the city of Port Augusta (Fig. 1); by the 1960s the capacity had been increased to 330 MW. The cooling water discharge from this development resulted in surface water temperatures about 6°C above ambient near the power station, with only occasional incursions of the water to the intertidal regions (Ainslie *et al.* 1989).

In the late 1970s the decision was made to proceed with the development of a new power station of up to a possible 750 MW (Fig. 1), with the ultimate potential to discharge 4 million cubic metres of warmed seawater a day to the Gulf, more than doubling the volume of water discharged at 6°C above Gulf ambient (Ainslie *et al.* 1989), and with predictions of localised but noticeable increases in temperatures of gulf waters

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¹ HAILS, J. R. (1982) Submarine geology, sediment transport, hydrodynamics and quaternary history of northern Spencer Gulf, South Australia. Seminar on the Research Needs for Management of the South Australian Gulfs, Australian Marine Sciences and Technologies Committee, Adelaide, 10 November 1982, 45-52. Unpubl.

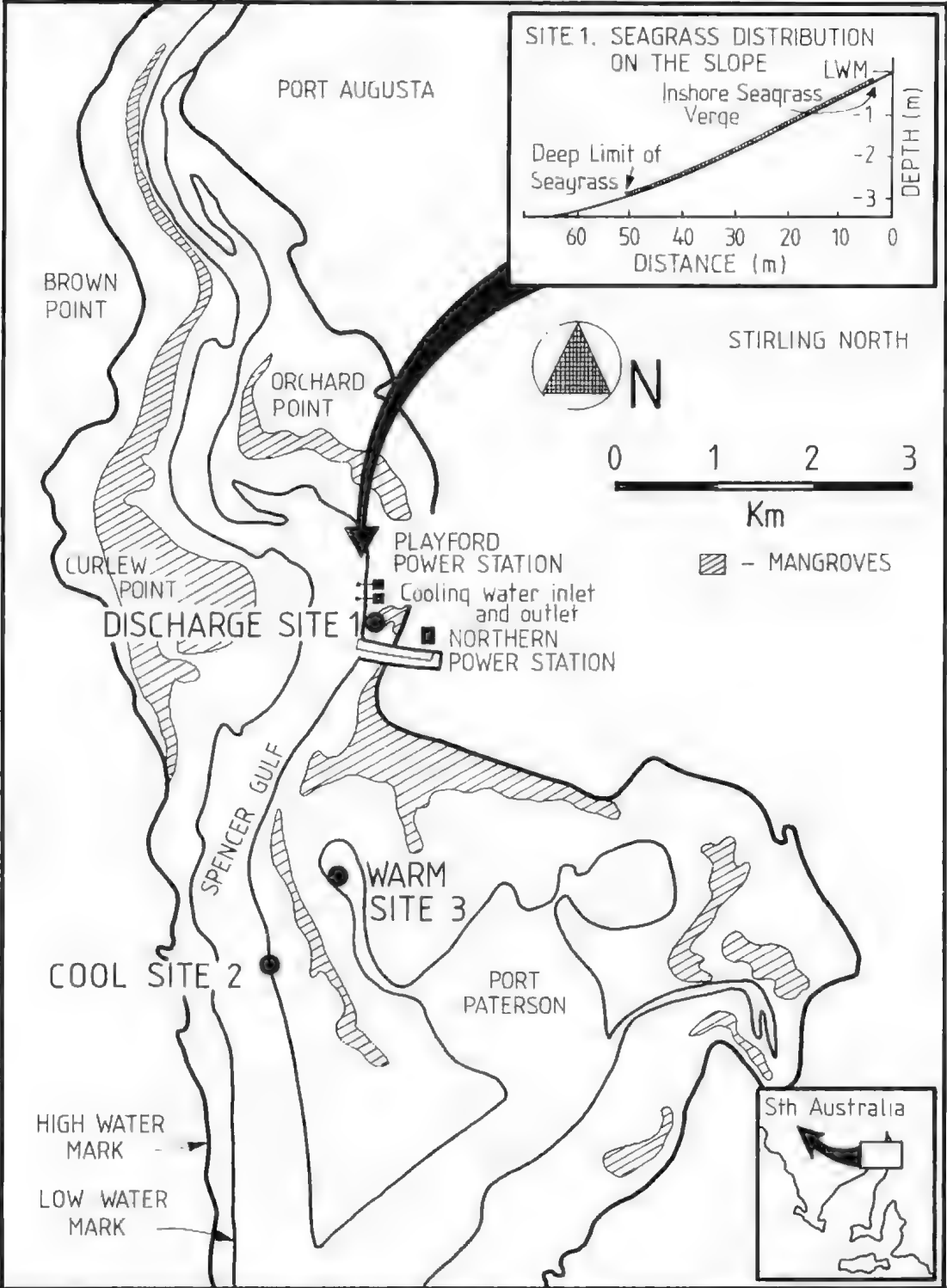


Fig. 1 Northern Spencer Gulf South Australia. Seagrass monitoring sites: (1) power station thermal discharge (2) Gulf ambient site remote from the discharge, and (3) Pt Paterson. Inset: seagrass distribution from low water mark to the Gulf channel at site 1

Under some tidal conditions short term maxima were predicted to exceed 30°C in the vicinity of the power station outfalls².

The reported effects of thermal discharges on seagrasses range from large scale devastation resulting from temperature increases only a few degrees Centigrade above summer ambient (Thorhaug *et al.* 1978), to reduction in seagrass density (Robinson 1987) and changes in specific growth characteristics such as leaf thickness and biomass (Vicente 1977). Circumstantial evidence suggests that relatively small changes in temperature of inshore waters may also have indirect effects on seagrasses through increased bacterial and fungal attack (Rasmussen 1977).

Once seagrass meadows begin to deteriorate, erosion, siltation and reduction in water clarity may lead to a decline in the seagrasses beyond the direct influence of the discharge (Shepherd 1986). Other secondary effects such as increased impacts of grazing organisms may also accelerate the decline of seagrasses under stress (Shepherd *et al.* 1989).

Both *Posidonia australis* and *P. sinuosa* occur in northern Spencer Gulf but the latter species is dominant in the inshore meadows near the power stations.

This paper describes the result of a monitoring programme conducted to assess the effects of the increased thermal effluent from the first 500 MW development of Northern Power Station on the growth of the seagrass *P. sinuosa*, in the light of predictions of localised water temperature extremes approaching, or even exceeding, the upper known field temperatures for this species².

Materials and Methods

Preliminary field work was undertaken in the 1986-1987 summer season to establish sampling techniques. The results of the seagrass monitoring programme for the period 1987-1989 are reported in this paper.

Water temperatures and growth of *Posidonia sinuosa* were measured at three sites in northern Spencer Gulf (Fig. 1). The Gulf sites were established on transect lines, the elevation and location of which were confirmed relative to an established Port Augusta Power Station datum as part of a contiguous study of the benthic infauna of the northern Gulf (Ainslie *et al.* 1989). Site 1 is within 200 m of the power station and within the influence of the thermal plume of the new Northern Power Station; Site 2 is on the eastern side of the Gulf, 3.5 km south of the power station

and beyond the predicted influence of the discharge plume². Site 3 is in Port Paterson, a large shallow embayment, also beyond the predicted influence of the thermal plume. The naturally high water temperatures which have been recorded in Port Paterson² can be attributed to the insolation of the extensive surrounding mudflats.

20 m transects were established at each site about 5 m seaward of, and parallel to the inshore seagrass verge, all at a depth of about 0.3-0.5 m below LWD (a depth of up to 3.5 m during the highest tides).

At each site *in situ* water temperatures were recorded within the leaf blade canopy with portable data loggers in custom-built PVC waterproof housings, and fitted with 15 k thermistor detectors.

Air temperatures were recorded at the South Australian Bureau of Meteorology weather station located on the Northern Power Station site.

Our object was to estimate several measures of the biomass and growth rate of seagrass.

A wide range of sampling quadrat areas is cited in the literature for seagrass studies, depending on the leaf blade density, and the need to ensure that an adequate number of leaf blades is tagged for measurement. Shepherd (1983) used sub-samples of 50 leaf blades for detailed measurements of *Posidonia australis* leaf blade lengths and widths in Spencer Gulf. More recently Pollard & Greenway (1993) used samples of between 20 and 60 shoots in a leaf marking study of the productivity of three species of seagrasses in the warm waters of Cairns Harbour, Queensland. In this study 15 cm² steel framed quadrats were used to define measurement areas for each sampling site. Preliminary collections in the summers of 1985 and 1986 yielded information on the leaf blade numbers for the quadrat area. Sixty nine quadrats, randomly placed along the transect lines, were sampled at all locations; the mean number of leaf blades/quadrat was 34.5 ± 17 . A decision was made to proceed with the field studies using five quadrats per site (averaging 170 blades/site). The sampling area/site was 1125 cm², comparable to that of a number of other productivity studies of seagrasses with a similar growth habit (Zieman 1974; Thorhaug *et al.* 1978; Walker & McComb 1988).

Within the quadrats all seagrass blades were tagged and harvested using methods outlined in Zieman (1974). Harvesting was carried out at high tide, approximately every six weeks depending on weather conditions and underwater visibility.

Total blade lengths, incremental growth (length) and dry biomass of whole blades and incremental growth (productivity) were recorded for each harvest. Numbers of new shoots, i.e. shoots which grew subsequent to the initial tagging, and their growth and dry biomass were also recorded. A simple "shoot index" is derived which is the number of new

² Electricity Trust of South Australia (1985) Northern Power Station Environmental Impact Statement, August 1985. Prepared by Kinhill Swarms, Unpubl.

shoots/m² (of seafloor area)/day expressed as a percentage of the original number of leaves tagged/m² for each sampling site. Blade widths were also recorded but were only used as a verification of the species collections.

Dry biomass was determined by drying freshly harvested blades to constant weight at 105°C, after removal of epiphytes with a stainless steel scraper and treatment in a 5% hydrochloric acid solution.

Results

Figure 2 presents a comparison of the Port Augusta summer air temperature and water temperatures at sites 1 to 3 during the summer of 1987-1988 with a 500 MW power station operating.

In the shallow seagrass beds of northern Spencer Gulf, air temperatures strongly influence the patterns of variation in the water temperatures at all three sites.

In mid-summer average water temperatures at all sites are between 20 and 25°C (Inset Fig. 2). Short term fluctuations are most pronounced at site 3 in the shallow bay of Pt Paterson, and least evident at the Gulf ambient site 2. Overall, summer water temperatures are marginally higher at site 1 near the thermal discharge than at the Gulf ambient site, but consistently highest at site 3 in Pt Paterson (Fig. 2).

At all sites, despite the high summer temperatures, seasonal temperature variation is typical of temperate regions with winter water temperature dropping below 15°C, even at site 1 adjacent to the power station outfall.

The summer relativity of the water temperatures between the sites does not persist throughout the year. During the cooler months, Gulf ambient temperatures fall significantly below those of Port Paterson, which in turn is cooler than site 1 adjacent to the power station outfalls.

Productivity (mean growth, dry weight/m²/d) of *Posidonia sinuosa* at sites 1 to 3, from November 1986, to August 1990, is shown on Fig. 3.

At the Gulf ambient site 2, and at site 1 near the power station cooling water outfall productivity shows a pronounced seasonal cycle with peaks between October and April. Although the seasonal cycle is less obvious in the seagrasses of the naturally-warmed site in Port Paterson, highest productivity values at this site were recorded in summer (Fig. 3).

Productivity was consistently highest at the Gulf ambient site 2 and least at site 3 in Port Paterson, with highest recorded productivity being 3.7 ± 1.1 g/m²/d, 3.1 ± 0.5 g/m²/d, and 1.6 ± 0.3 g/m²/d at sites 2, 1, and 3 respectively (Fig. 2).

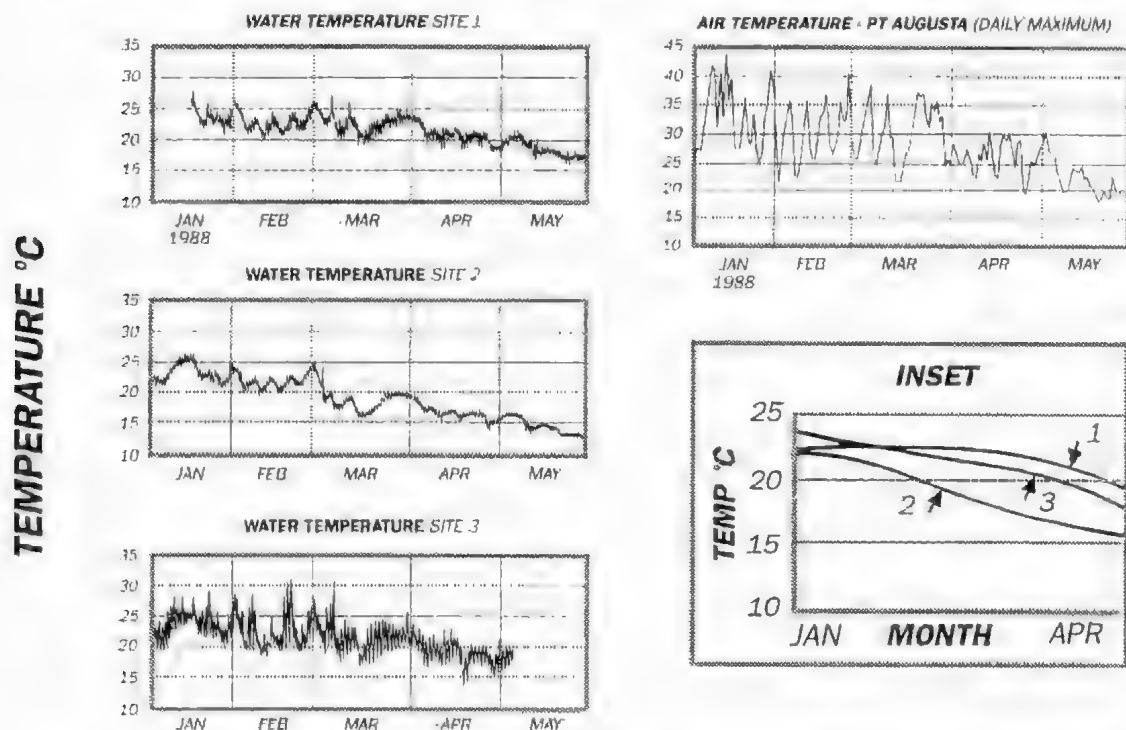


Fig. 2. Maximum daily air temperatures at the S.A. Bureau of Meteorology Station Port Augusta, and three hourly maximum water temperatures in the seagrass canopy at sites 1, 2 and 3 (inset: water temperatures, lines of best fit (polynomial least squares regression) at sites 1 to 3).

Productivity data for each site were compared, no *a priori* attempt being made to discern seasonal "cut-offs". Variances were not homogeneous (Bartlett's test, $P < 0.01$), and analysis of variance was therefore not used. However Kruskal-Wallis analysis showed significant differences between all three sites ($P < 0.01$),

the greatest difference being between sites 3 and 1 and between sites 3 and 2 (Fig. 3).

Maximum mean standing biomass also occurs in summer (Fig. 4). As with productivity, the seasonal cycle is most pronounced at the cool Gulf ambient site 2, and least pronounced at site 3. The highest standing

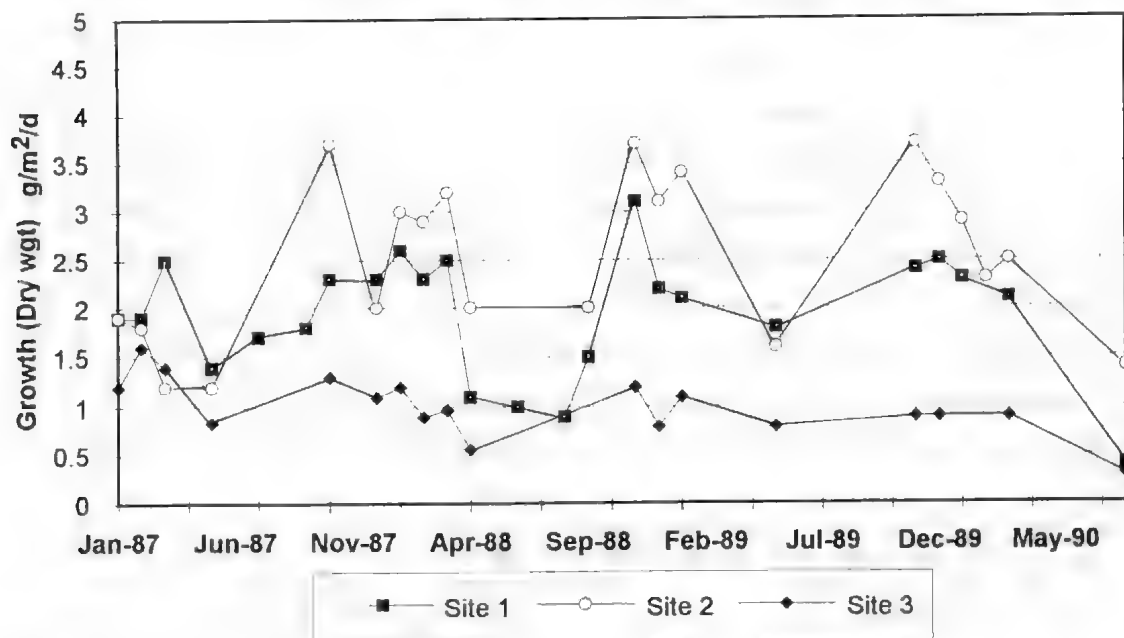


Fig. 3. Seagrass productivity, leaf blades, $\text{g/m}^2/\text{d}$ (dry weight) at sites 1, 2 and 3.

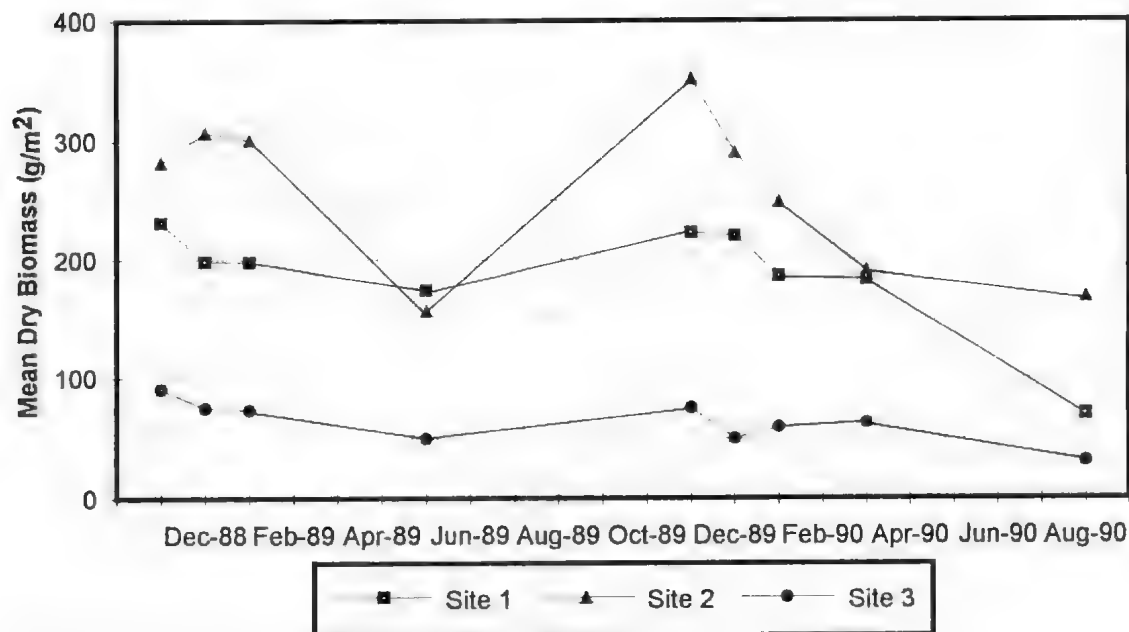


Fig. 4. Seasonal variation in mean standing biomass, leaf blades, g/m^2 (dry weight) at sites 1, 2 and 3.

biomass was recorded at site 2 in November 1989, 352 g/m². The highest summer mean standing biomass recorded at site 1 nearest the outfall was 231 g/m². In November 1988, while the mean standing biomass is consistently lower at site 3 in Port Paterson than at the other two sites with a summer maximum of 91 g/m² (Fig. 4). In November 1988, Analysis of variance using transformed data (\log_{10}) indicated significant differences between the standing biomass data of each of the three transects ($P < 0.01$). An *A posteriori* multiple comparison test (Sokal & Rohlf 1969) indicated that although the differences between sites 3 and 2 and 3 and 1 were significant, sites 1 and 2 were not significantly different.

Comparisons were made of total blade lengths and blade growth rates for sites 1, 2 and 3 after combining the data collected for these measurements for January 1988 and January 1989.

Mean blade lengths were 438.9 ± 161.3 mm, 316.0 ± 95.0 mm, and 135.8 ± 50.3 mm at sites 2, 1 and 3 respectively (significantly different, ANOVA, $F = 367.6$, $F_{0.05, 2, 804} = 3.0$).

Mean summer growth rates (incremental blade length) were 4.7 ± 2.8 mm/d, 3.6 ± 1.8 mm/d and 1.9 ± 1.1 mm/d at sites 2, 1 and 3 respectively. As with blade lengths there were significant differences between the sites (ANOVA, $F = 254.0$, $F_{0.05, 2, 1881} = 3.0$).

⁴ Hosi, W. M. (1977) Marine Biological Studies in Relation to the Operation of the Torrens Island Power Station. MSc. Thesis, Adelaide University, Unpubl.

Shoot production occurs all year round; the shoot index is highest at all sites during summer. Shoot indices are similar at sites 1 and 2, while the shoot index at site 3 is consistently much higher (about 2 to 3 times as high) than at the other two sites (Fig. 5).

Although no measurements were taken, field observations suggest that the epiphytic growth was consistently higher at site 1 near the outfall than at the gulf-ambient site 2, and higher again at site 3 in Pt Paterson. This was particularly evident for the serpulid worm *Eulospira convexis*, a species which has previously been demonstrated to thrive in the thermal outfall at Torrens Island Power Station in the Pt. River estuary, South Australia³.

Discussion

A number of studies have indicated the susceptibility of seagrasses in subtropical regions to water temperature increases above ambient (Thorhaug *et al.* 1978; GESAMP 1984). In particular, there is evidence that many organisms, including seagrasses, are living close to the upper limits of their thermal tolerance during the warmest part of the year, and even short periods above the summer maxima can have significant adverse impacts (Zieman 1974; GESAMP 1984).

Larkum & Den Hartog (1989) hypothesise that the current distribution of species of the genus *Posidonia* in temperate regions, and the lack of evidence that any *Posidonia* species has ever occurred in tropical conditions in the past, may indicate that species of this genus have more limited temperature tolerance than species which occur in the tropics.

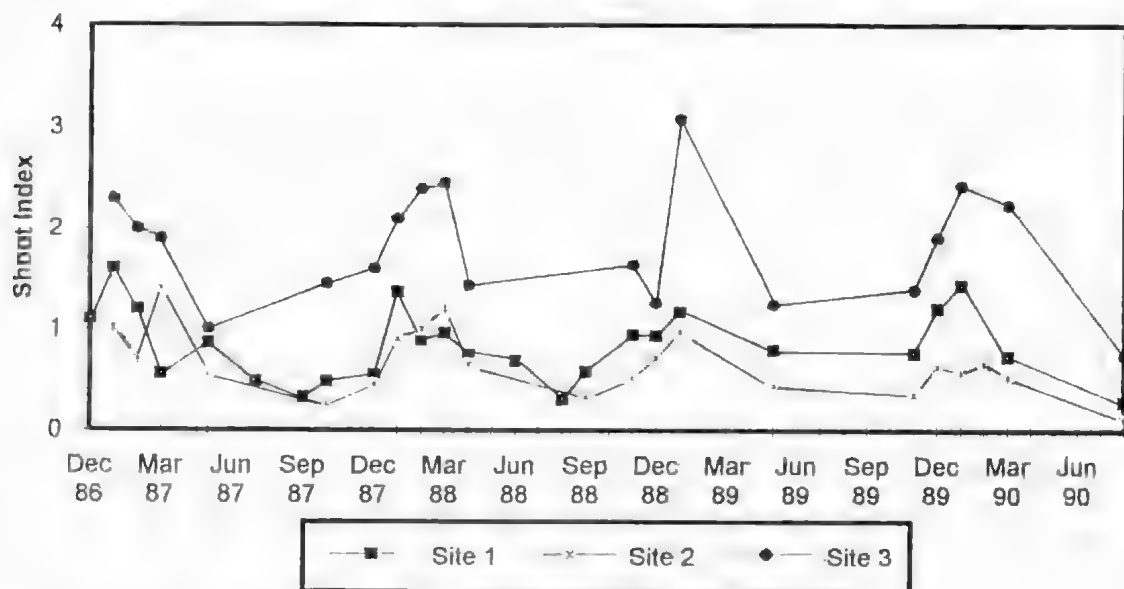


Fig. 5. Seasonal variation in shoot index (number of new shoots/m² d as a percentage of the original number of leaf blades per m² at the time of tagging) at sites 1, 2 and 3.

In northern Spencer Gulf, although seasonal water temperatures range from as low as 11°C in winter to the mid to high 20s during summer (Ainslie *et al.* 1989), the high summer water temperatures are more typical of subtropical conditions than those normally associated with temperate coastal waters of the southern Australian coastline. (Subtropical conditions are defined as those where water temperatures generally range from 20-25°C, and do not exceed 30°C [GESAMP 1984]).

During mid summer, when air temperatures range to 45°C, the water temperature in the seagrasses at the outfall (site 1) is consistently about 0.5-1.5°C higher than at Gulf ambient site 2 (inset Fig. 2). The difficulty in defining local ambient water temperatures is, however, illustrated by the difference between site 2 and site 3 on the southern shores of the large shallow embayment of Port Paterson. The latter site is also beyond the influence of the thermal plume, but exhibits consistently high average summer temperatures (inset Fig. 2), up to 2°C warmer than Gulf ambient (inset Fig. 2).

Comparison of summer temperature regimes between sites is complicated by the short term occurrence of extreme temperatures. Short term maximum temperatures at site 1 (28°C on two occasions, Fig. 2) are about 1°C higher than those recorded at the Gulf ambient site, and as high as the maximum field temperatures recorded prior to this study for Australian *Posidonia* species (Walker & McComb 1988). At site 3 which has the most pronounced diurnal variations the short term maxima recorded during summer exceeded 30°C on a number of occasions, more than 3°C higher than the peak temperature at the Gulf ambient site 2 (Fig. 2), and the highest field temperatures at which *Posidonia* species have been recorded.

Although seasonal data have been unavailable for *Posidonia sinuosa*, information on the productivity of a number of different species of seagrasses has been reviewed by Walker & McComb (1988) and Hillman *et al.* (1989). These authors found that seagrass species in temperate waters in general tend to show a pronounced seasonal variation with a distinct growing season in summer. However Walker & McComb (1988) found no clear seasonal pattern in the productivity of *Posidonia australis* in the semi-enclosed bays of Shark Bay, Western Australia, over a one year period. The water temperatures in Shark Bay ranged from about 18°C to more than 26°C, and maximum temperatures up to about 28°C have been recorded in this area (Walker & McComb 1988). Despite the fact that at all three sites in the present study summer water temperatures resembled the semi-tropical conditions of Shark Bay, the *P. sinuosa* growing at Gulf ambient (site 2) and in the marginally warmer conditions adjacent to the power station thermal discharge (site

1), show seasonal fluctuation in both productivity and standing biomass, with maxima for both measures in the warmer summer months. Even at site 3, with the most extreme conditions, summer 'peaks' are evident in these features, although seasonal patterns are not as pronounced as at the other two sites. This persistence of summer peaks in productivity and standing biomass, particularly at sites 1 and 2, suggests that the *P. sinuosa* of northern Spencer Gulf may be more tolerant of extreme summer conditions than, for example, the *P. australis* of Shark Bay.

At all sites there was some variation between the values recorded from year to year for summer peaks of both productivity and standing biomass. This variation was, however, no more pronounced than natural year to year variations recorded in a number of recent studies of a range of temperate Australian seagrasses (Walker & McComb 1988; Hillman *et al.* 1989). Although the growth of the seagrass *P. sinuosa* differs between the three sites, the inter-annual comparisons indicate that, at any given site, the growth is comparable from year to year. There is no evidence of "deterioration" at site 1 adjacent to the power station, or at either of the two control sites, during the course of the current study.

Although numerous studies have documented the range of effects that artificially imposed temperature regimes may have on seagrasses, few have attempted to describe the progressive effects on growth characteristics which occur with incremental temperature increases above ambient. The exception is that of Thorhaug *et al.* (1978) who recorded detailed changes in growth of leaf blades, productivity and standing biomass (standing crop) in tropical and subtropical *Thalassia* stands subjected to incremental increases in water temperature above ambient.

Accepting that different species may have quite different temperature tolerances, it is nevertheless of interest to examine the similarity between *Thalassia* species with a subtropical distribution, and *P. sinuosa*, subjected to above-ambient temperatures in an environment where summer temperatures are already high in terms of the geographic distribution of this temperate species.

Thorhaug *et al.* (1978) report that, with increases as little as 1.5°C above summer ambient water temperature, growth per blade, productivity, and standing biomass of *Thalassia* declined to 64%, 60% and 82% respectively, of that at ambient temperatures and continued to decline sharply with incremental increase in above-ambient temperature. At 5°C above ambient the seagrass "disappeared" from the area (Thorhaug *et al.* 1978).

The maximum mean productivity recorded for *P. sinuosa* at site 1, with average summer water temperatures 0.5-1.5°C above Gulf ambient and short term peak temperatures up to 1°C higher than short

term Gulf ambient peak temperatures, was 84% of that recorded at site 2. A contributing factor to this lower productivity is the lower rate of blade growth at site 1, mean growth per blade being only about 77% of that of blades at site 2 during the warmest time of the year. Despite the fact that over the period December 1988 to August 1990 standing biomass of *P. sinuosa* at site 1 was not statistically significantly lower than at site 2, the maximum mean standing biomass recorded during this period at site 1 was only about 70% of the maximum recorded during the same period at site 2 (Fig. 4).

At site 3 in Port Paterson with average temperatures consistently 2°C higher than Gulf ambient and peak temperatures 3°C higher than ambient peaks, productivity, standing biomass, total blade length, and blade growth are all significantly lower than at the Gulf ambient site (only 30-40% of Gulf ambient values for maximum mean productivity (Fig. 3), maximum mean standing biomass (Fig. 4), and mean summer blade lengths and growth rates).

There is a lack of published information on *P. sinuosa* with which to compare the growth information from the present study. Neverauskas (1988) examined the effects of shading on a mixed *P. sinuosa* and *P. angustifolia* stand at a depth of 11-12 m, in an area removed from any land based discharge. In winter, at the commencement of the shading experiments Neverauskas recorded a mean standing biomass of 100 g/m². In this study the winter standing biomass of *P. sinuosa* at both sites 1 and 2 ranged from about 125 g/m² to 175 g/m², while the winter standing biomass at site 3 in Pt Paterson was about 50 g/m² (Fig. 4). Accepting that comparisons made between seagrasses from different localities and depths can be misleading (Ainslie 1989) these biomass values nevertheless suggest that the seagrass stands at both site 1 and site 2 are at least as vigorous as in a location deliberately chosen for its apparent "health". The *P. sinuosa* at site 3 in Pt Paterson, on the other hand, is less vigorous not only in comparison with the other sites in the northern Gulf, but also in comparison to that examined by Neverauskas (1988).

This paper does not rule out the possibility that, in the higher water temperatures at site 1, and particularly at site 3, indirect factors lead to the reductions in seagrass growth. For example Neverauskas (1988) has shown that shading of a mixed *Posidonia sinuosa* and *P. angustifolia* stand with shade cloth (to simulate epifaunal growth on the leaf blades) resulted in significant decline in standing biomass (standing crop), and leaf blade length. It is possible that indirect effects from shading caused by relatively greater epiphytic growth at site 1, and particularly site 3, may have contributed to the reduced productivity, leaf blade length and growth, and dry biomass at these sites compared to site 2.

Neverauskas (1988) also found that with progressive periods of shading, the shoot density declined, suggesting a reduction in the appearance and growth of new shoots. In the present study new shoot production (with respect to leaf blade density) was very similar at sites 1 and 2 throughout the year. Particularly during the summer, however, new shoot production as a proportion of the leaf blade population was 2 to 3 times higher at site 3 in Port Paterson than at the other two sites. If shading by epiphytic growth is a contributing factor to the observed reduction of standing biomass and productivity in this study the comparison to the results of Neverauskas (1988) does not extend to new shoot production. However, while in Neverauskas's study whole shoots were shaded, in this study the epiphytic growth shaded individual leaves, with more shading of older leaf blades. Although it seems likely that this shading by epiphytes contributes to a reduction in standing biomass and productivity, the consistently higher relative production of new shoots at site 3 suggests a response similar to that of terrestrial grasses, where cutting back to reduce shading by old leaves can result in increased leaf production, tillering and branching (Hendrick & Black 1986). The stunted growth of older leaf blades at site 3 may expose the new blades to more light. One result of this higher shooting frequency in Port Paterson is that, despite the stunted growth of the *P. sinuosa*, the shoot density does not decline; there is no ongoing deterioration of the stands as observed by Neverauskas (1988) in artificial shading experiments.

Salinities at all three sites are high, as they are throughout the northern Spencer Gulf, in summer reaching about 48 (Nunes & Lennon 1986). Although information on the salinity tolerance of *P. sinuosa* is not well documented, *P. australis* survives in a wide range of estuarine salinities up to 57 (Cambridge & Kuo 1979). Tyerman *et al.* (1984) have shown that the salinity tolerance of *P. australis* is, in part, due to the physical shielding of the sheaths of older leaf blades surrounding the bases of the youngest lamina. The leaf sheaths of *P. sinuosa* are at least as robust as that those of *P. australis* (Cambridge & Kuo 1979) suggesting that the same mechanism for salinity tolerance operates in this species. Although this paper does not rule out the fact that a combination of factors (high temperature and high salinity) may lead to the stunting of the seagrasses in Port Paterson, the high water temperatures would appear to be the key variable between the sites.

From their studies of thermal effects on *Thalassia* Thorhaug *et al.* (1978) suggest tentatively that increases above ambient water temperatures of about 1.5°C may be considered "rational" with respect to the limited impact on seagrass and associated communities. In the current study, the maximum summer temperatures at site 1, near the thermal discharge, fall within this

category. The results of this study also support the contention that the overall change in *P. sinuosa* growth is relatively minor with this magnitude of temperature increase above ambient, less than the order of change considered acceptable by Thorhaug *et al.* (1978) for *Thalassia*. In Pt Paterson, in consistently higher above-ambient summer water temperatures than recorded near the thermal outfall, *P. sinuosa*, although exhibiting stunted growth characteristics of this species in marginal environments (Cambridge 1974; Cambridge & Kuo 1979), persists with no indication of ongoing decline, in terms of biomass, productivity, leaf blade growth and length, or areal extent of local distribution.

It has been proposed that the sediment stabilising role of seagrasses may be particularly important in maintaining the integrity of the sloping banks of the channel of northern Spencer Gulf¹. While the stunted seagrasses on the relatively protected shores of Pt Paterson survive without any evidence of ongoing

decline, if the seagrasses in the more exposed Gulf channel (for example adjacent to the thermal outfall) were to be subjected to further, small summer water temperature increases, resultant stunted growth could lead to increased localised mobilisation of the shoreline sediments. This, in turn, could lead to longer term effects on the spatial distribution of seagrasses in this area. Given this possibility, any consideration of future development of the power station should recognise the need to ensure that there is no increase in the maximum temperature of the discharged cooling water.

Acknowledgments

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TRANSACTIONS OF THE

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**POPULATION AND REPRODUCTIVE ECOLOGY OF THE
SMALL-MOUTHED HARDYHEAD *ATHERINOSOMA
MICROSTOMA* (GÜNTHER) (PISCES: ATHERINIDAE)
ALONG A SALINITY GRADIENT IN THE COORONG,
SOUTH AUSTRALIA**

BY ROBYN L. MOLSHER, MICHAEL C. GEDDES* & DAVID C. PATON**

Summary

Molsher, R. L., Geddes, M. C. & Paton, D. C. (1994) Population and reproductive ecology of the small-mouthed hardyhead *Atherinosoma microstoma* (Günther) (Pisces: Atherinidae) along a salinity gradient in the Coorong, South Australia. Trans. R. Soc. S. Aust. 118(4), 207-216, 30 November, 1994.

Atherinosoma microstoma in the Coorong exhibited a one-year life cycle with multiple spawning over a four month breeding season from September to December. Large numbers of larval and juvenile fish (5-15 mm long) appeared in samples during October and November and grew rapidly over summer, most reaching lengths of 26-35 mm by autumn and 36-45 mm by the following spring. Only one ovary developed in females and this began to enlarge during August when batches of eggs began maturing. Gonosomatic indices also began to increase at this time. Female fish with spent ovaries were first caught in November. The numbers of large hardyheads (>35 mm) in samples declined in December and January, reflecting post-breeding mortality.

Key Words: *Atherinosoma microstoma*, Coorong, hardyhead, salinity, reproduction, population biology, fecundity.

POPULATION AND REPRODUCTIVE ECOLOGY OF THE SMALL-MOUTHED HARDYHEAD *ATHERINOSOMA MICROSTOMA* (GÜNTHER) (PISCES: ATHERINIDAE) ALONG A SALINITY GRADIENT IN THE COORONG, SOUTH AUSTRALIA

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Summary

MÖLSHER, R. L., GEDDES, M. C. & PATON, D. C. (1994) Population and reproductive ecology of the small-mouthed hardyhead *Atherinosoma microstoma* (Günther) (Pisces: Atherinidae) along a salinity gradient in the Coorong, South Australia. *Trans. R. Soc. S. Aust.* 118(4), 207-216, 30 November 1994.

Atherinosoma microstoma in the Coorong exhibited a one-year life cycle with multiple spawning over a four month breeding season from September to December. Large numbers of larval and juvenile fish (5-15 mm long) appeared in samples during October and November and grew rapidly over summer, most reaching lengths of 26-35 mm by autumn and 36-45 mm by the following spring. Only one ovary developed in females and this began to enlarge during August when batches of eggs began maturing. Gonosomatic indices also began to increase at this time. Female fish with spent ovaries were first caught in November. The numbers of large hardyheads (> 35 mm) in samples declined in December and January, reflecting post-breeding mortality.

Salinities ranged from 9 to 67 g L⁻¹ at Noonameena, the most northerly sampling site, and from 35 to 94 g L⁻¹ at Tea Tree Crossing in the southern end of the Coorong lagoon system. High salinities did not have a marked effect on the population ecology or reproductive potential of *Atherinosoma microstoma*. Hardyheads were caught at all sites on all sampling occasions and no marked differences were found in fish size, growth rate, condition or relative hatch fecundity for fish caught from different localities along the salinity gradient. Hardyheads were coping well with the high and fluctuating salinities that exist in the Coorong. Significant differences in hatch fecundity were found between years, with those in spring 1990 being about half those of 1991, perhaps reflecting differences in food availability. The possible effects of future proposed reductions in salinity for the Coorong on the biology of *A. microstoma* are discussed. Changes in salinity are unlikely to limit the distribution of hardyheads except through possible influences on their food supply.

KEY WORDS: *Atherinosoma microstoma*, Coorong, hardyhead, salinity, reproduction, population biology, fecundity.

Introduction

The Atherinidae (hardyheads) is a widespread family of small fishes that are commonly found in calm, shallow waters and often have short life cycles (e.g. Gon & Ben-Tuvia 1983; Prince *et al.* 1982; Prince and Potter 1983; Potter *et al.* 1983, 1986). Atherinids are often euryhaline but high salinity may affect their population and reproductive biology. For example, suspected dwarfing in the Mediterranean atherinid, *Atherina boyeri*, may be associated with high salinities (Gon & Ben-Tuvia 1983). The North American atherinid, *Atherinops affinis affinis*, spawned in the field at salinities of 72 p.p.t. but the young died within four months (Carpelan 1955). Most fish species in the Laguna Madre of Texas (up to 80 p.p.t.) do not spawn at salinities greater than 45 p.p.t. (Hedgepeth 1967). Generally, high salinities and fluctuations in salinity restrict reproduction in many aquatic animals, affecting both the number of offspring produced and the timing and length of the breeding season (Kinne 1964).

The small-mouthed hardyhead, *Atherinosoma microstoma* (Günther), is found in abundance over a wide range of salinities including estuaries, marine embayments and hypermarine lagoons in south-eastern Australia from the Tuggerah Lakes in New South Wales, southwards and westwards to Spencer Gulf in South Australia (Ivantsoff 1978¹; McDowall 1980; R. Connolly & G. K. Jones pers. comm.). The maximum sizes approach 90 mm (total length) in Tasmania and 80 mm in Victoria (Cadwallader & Backhouse 1983). The life cycle of *A. microstoma* has been studied in Dee Why Lagoon, N.S.W., where salinities ranged from 3 to 13 p.p.t. (Potter *et al.* 1986). In these estuarine conditions, *A. microstoma* exhibited a one-year life cycle with a four-month breeding season during spring (August to November). Fry entered the trappable population in October, while larger adults rapidly declined in abundance after November. Growth effectively ceased over autumn and winter (April to August).

A. microstoma has been found throughout the Coorong where conditions range from estuarine in the north to hypersaline in the south (Geddes & Butler 1984). Although hardyheads have been caught in the Coorong in excess of 100 p.p.t. TDS (total dissolved solids), equivalent to a salinity of 91 p.p.t., Geddes (1987) has suggested that extremely high salinities

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¹ IVANTSOFF, V. (1978) Taxonomic and systematic review of the Australian fish species of the family Atherinidae with references to related species of the old world. Unpublished PhD Thesis, Macquarie University.

(>100 p.p.t. TDS) during late summer and autumn may restrict the southerly distribution of these fish in the Coorong in some years. This study takes advantage of the longitudinal gradient of salinity that exists in the Coorong to study the effect of high salinity on the reproductive performance and population structure of *A. microstoma*.

Materials and Methods

The population structure and reproductive biology of hardyheads were studied at five sites within the Coorong: Noonameena, Villa dei Yumpa, Policemans Point, Salt Creek and Tea Tree Crossing (Fig. 1). These sites spanned a 65 km length of the Coorong lagoon system, with Noonameena in the north usually experiencing a lower range of salinities than the other four sites that were further south (Geddes 1987). The southernmost site, Tea Tree Crossing, was at the

southern extremity of permanent water in the Coorong where the highest salinities in the Coorong had been reported.

The salinities and temperatures of the water at each of the sites were measured at monthly intervals between September 1990 and January 1992. Water temperatures were recorded at a depth of 40 cm between 0900 h and 1800 h. Water samples, collected from a depth of 40 cm, were returned to the laboratory and salinities were estimated by measuring electrical conductivities (conductivity meter CDM3) and converting these values to salinities using tables from Williams (1986). Samples with conductivities over 100 mS cm⁻¹ were diluted and the calculated salinities multiplied by the dilution factor.

Each month, fish were caught from each site using a 5.5 m long, 1.75 m deep seine net with a mesh size of 1.9 mm. All seining was conducted at a depth of 0.2–0.8 m with hauls over a distance of 40 m. On most occasions a single haul was taken but when the sample contained low numbers of fish (<50), additional seines were undertaken. Successive seines in the one area showed no significant difference in the mean length of fish caught ($t = 1.348$, $N = 200$, $P = 0.179$). Fish traps (63 by 36 by 36 cm, mesh size 1.9 mm) baited with meat (usually chicken) and set overnight in water 0.4–0.8 m deep, were used in the first six months of the study. Traps were expected to catch larger fish, whose superior swimming ability may have enabled them to escape the seine net, and thus provided information on the larger adults in the population. They also provided additional fish for assessing reproductive condition. In addition, a plankton net (350 µm mesh, 60 cm diameter) was hauled through the water (depth 0.2–0.6 m) for two minutes to check for the presence of larval *A. microstoma*. Fish were immediately preserved in 10% buffered formalin and returned to the laboratory where their length and reproductive condition were measured.

The total length (TL—tip of snout to end of caudal fin) of each fish from both the seine and trap samples was recorded to the nearest millimetre using dial calipers. Where the number of individuals was large, a random subsample of approximately 150 individuals was measured. The standard length (SL—tip of snout to posterior edge of the last lateral line scale) of a subsample of fish was measured to determine the relationship between TL and SL, thereby allowing comparisons with other studies. Lengths and body weights of hardyheads caught in October 1990, December 1990 and March 1991 at each of three sites (Noonameena, Policemans Point and Tea Tree Crossing) were measured so that length-weight regressions could be calculated. Fish condition was assessed by comparing these length-weight regressions between sites. All length and weight measurements were obtained from fish that had been preserved in 10%

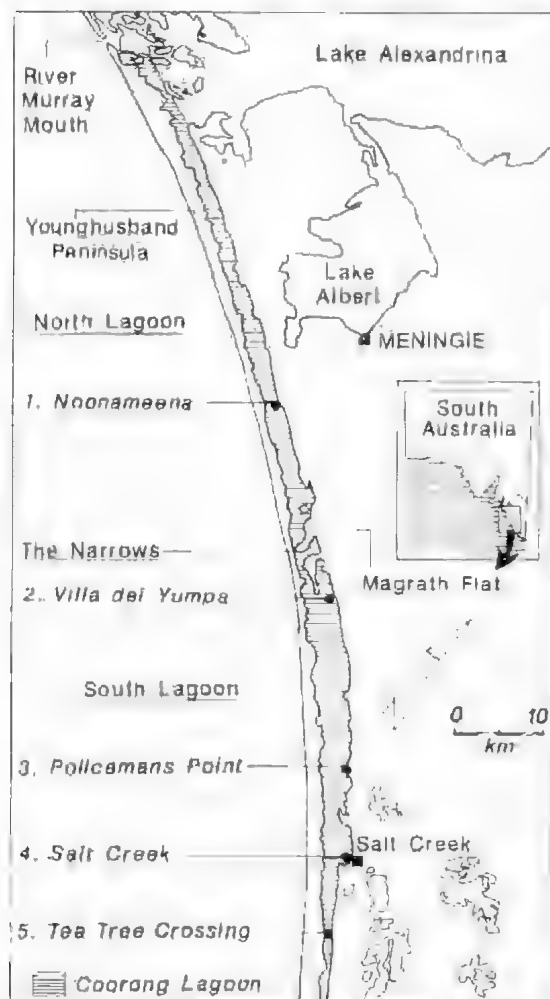


Fig. 1. The Coorong Lagoon showing the five sampling sites.

buffered formalin. Sex ratios were calculated for up to 50 hardyheads (>30 mm length) caught in each seine sample from October 1990 to May 1991. The sex of the fish was determined by macroscopic examination of the gonads. Gonads in fish <30 mm had not differentiated clearly and so these fish could not be sexed reliably. Orange coloration of the mid-lateral line and eyes was observed in some fish and the sex of 95 fish that exhibited this coloration was determined.

Seasonal patterns in the reproductive cycle of hardyheads were determined from changes in gonosomatic indices (GSI) and the examination of oocytes in the ovaries of female fish. Male fish were not investigated as preliminary examinations showed no marked changes in gonadal weight. The gonosomatic index (GSI) was calculated by expressing gonad weight as a percentage of body weight (De Vlaming *et al.* 1982). Gonad weight and body weight were measured to the nearest milligram for up to 20 female fish (TL > 40 mm) in each sample. Only female fish that were at least 40 mm in length were used in the analysis as the ovaries of smaller fish did not contain maturing oocytes. Ovaries of female fish from three sites (Noonameena, Policemans Point and Tea Tree Crossing) were excised and preserved in modified Gilson's fluid (Puckridge 1988²). These ovaries were then teased apart, shaken vigorously, and stored for two weeks to separate the oocytes from the ovarian tissue. Preliminary microscopic examination revealed three different egg types, which parallels the situation found for *Menidia menidia* (Conover 1985). The three general egg types were classified by size (oocyte diameter) and appearance as follows:

1. **immature oocytes:** 0.05-0.70 mm in diameter. The smaller oocytes in this group (0.05-0.22 mm) had a clear cytoplasm and large nucleus, while the larger oocytes (0.23-0.70 mm) were white, opaque and often irregular in shape.
2. **maturing oocytes:** 0.71-1.60 mm in diameter. Spherical and dark yellow in colour.
3. **ripe oocytes:** 1.61-2.50 mm in diameter. Spherical and hydrated with a yellowish yolk centre.

Diameters of oocytes were determined from a single measurement on a random orientation basis (West 1990) using a microscope-video attachment and a digitiser pad downloaded to a computer. Subsequent categorizations of oocytes were based only on appearance. Numbers of maturing and ripe oocytes in ovaries from samples over the two breeding seasons were counted using a stereo-dissecting microscope; immature oocytes were difficult to count and were only counted for samples of fish caught between September

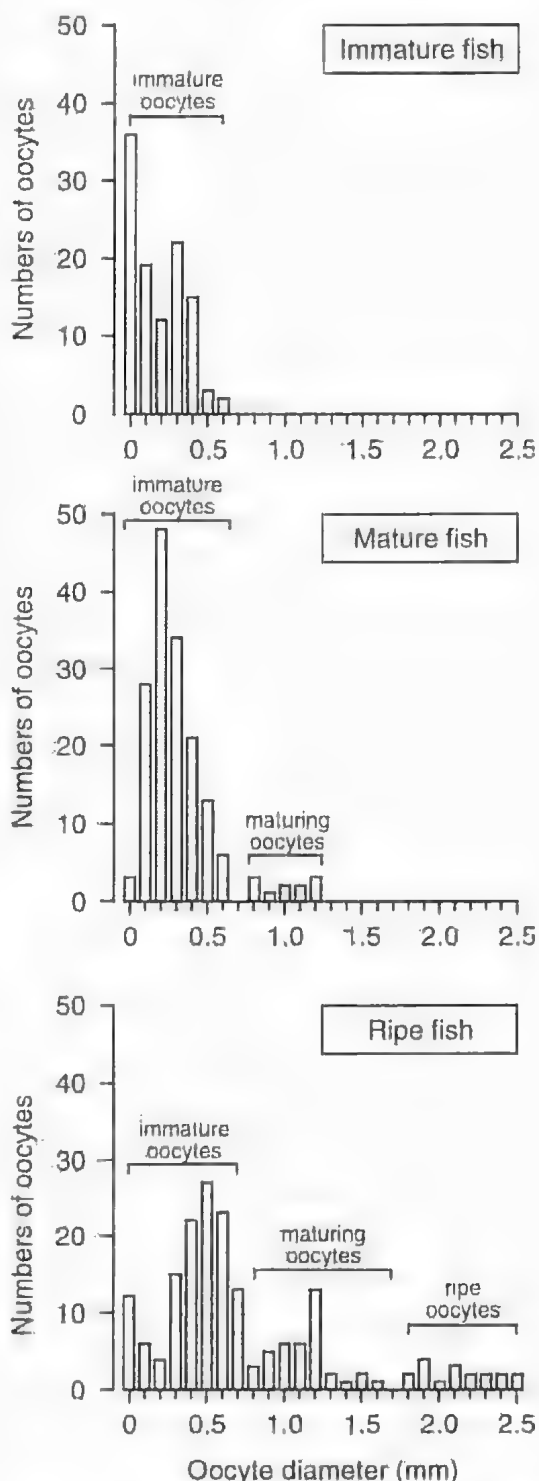


Fig. 2. Frequency of oocyte diameters from the gonads of an immature fish, a mature fish and a ripe fish.

² PUCKRIDGE, J. T. (1988) The life history of a gizzard shad, the bony bream, *Nematalosa erebi* (Günther) (Dorosomatinae, Teleostei) in the Lower River Murray, South Australia: MSc Thesis, University of Adelaide. Unpubl.

1990 and January 1991. Fish were classified into four stages depending on the type of oocytes present (Fig. 2);

1. **immature fish:** immature oocytes only, firm ovary.
2. **mature fish:** immature and maturing oocytes.
3. **ripe fish:** immature, maturing and ripe oocytes.
4. **spent fish:** maturing or ripe oocytes absent, flaccid ovary.

"Batch fecundity" was defined as the number of maturing oocytes in the ovary and presumably represented the maximum number of oocytes that could be ripened and subsequently spawned at one time. "Relative batch fecundity" was defined as the number of maturing oocytes per gram of ovary-free body weight (Conover 1985). Differences in the fecundity of female fish at different sites in the Coorong were assessed by comparing relative batch fecundities.

Results

Physical Characteristics of the Coorong — September 1990 to January 1992

A longitudinal gradient in salinity persisted in the Coorong with salinities increasing from Noonameena in the North Lagoon to Tea Tree Crossing at the southernmost end of the Coorong (Fig. 3). Hypersaline conditions (>35 g L⁻¹) were maintained at all sites in the South Lagoon, except briefly at Villa dei Yumpa in September 1991. At Noonameena, conditions were estuarine during winter and spring (9–32 g L⁻¹) and generally hypermarine during summer. Seasonal trends were also evident at all sites with salinities high in summer, falling in autumn and rising again in spring. In September 1990, salinities ranged from 32 g L⁻¹ at

Noonameena to 57 g L⁻¹ at Tea Tree Crossing, while in February 1991 salinities had risen to 60 g L⁻¹ and 94 g L⁻¹ at these two sites respectively. Seasonal changes in salinity were similar in the two years. However, salinities reached their minima earlier in 1991 (August/September) and were lower than in the previous year. Water temperature varied seasonally with maximum water temperatures in excess of 24°C recorded during late summer and minimum temperatures of 11°C in winter (Fig. 3).

Distribution of Fish in the Coorong

Hardyheads were collected from all sites throughout the 17 month period. The highest salinity at which they were found was 94 g L⁻¹ (Tea Tree Crossing, February 1991). Five other species of fish were caught commonly, yelloweye mullet (*Aldrichetta forsteri*), congolli (*Pseudophritis urvilli*), river garfish (*Hyporhamphus regularis*), greenback flounder (*Rhombosolea tapirina*) and blue spot goby (*Pseudogobius olivaceus*). All species were caught at Noonameena and Villa dei Yumpa where salinities were lower. However, yelloweye mullet was the only species caught with *A. microstoma* at Tea Tree Crossing, and then only during winter and spring. Yelloweye mullet, congolli and blue spot goby were caught at salinities up to 64, 83 and 87 g L⁻¹ respectively. Flounder and garfish were caught only at relatively low salinities (<36 g L⁻¹) and only on three occasions. *A. microstoma* far outnumbered other fish species in each sample.

Population Structure of *Atherinosoma microstoma* in the Coorong

The abundances of fish collected at the five sites on the 17 sampling occasions was analysed by two way analysis of variance. The number of hardyheads caught in the first seine for each sample was used in the analysis. There was no significant difference between sites ($F = 0.87$, d.f. = 79, $p > 0.05$) but there was a highly significant difference between sample dates ($F = 6.03$, d.f. = 79, $p < 0.001$). Greater numbers of hardyheads were caught during spring and summer. The length frequencies of fish in each sample were inspected and no consistent differences between sites were noted so the sites were pooled for length frequency analysis. The sizes of hardyheads were highly variable at any one time in the year, but there were distinct seasonal patterns (Fig. 4). Larvae and fry (5–15 mm; length class 1 of Fig. 4) were prominent in October, November and December (spring-early summer) of 1990 and 1991. At this time of the year, length-frequency distributions were often distinctly bimodal, consisting of small fish (<25 mm) and larger fish (>35 mm). The 1990 cohort of smaller fish showed a gradual increase in length during summer, reaching lengths of 26–35 mm (length class 3) by May

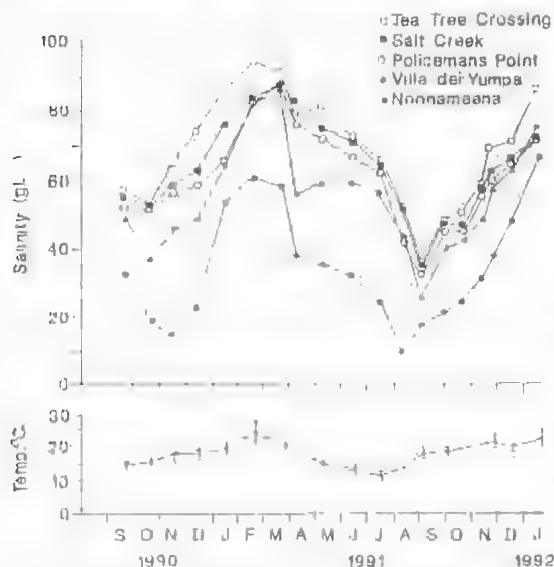


Fig. 3. Seasonal fluctuations in salinity and temperature at five sites in the Coorong Lagoon. Salinities are shown for each site and temperatures are shown as the mean and range for the five sites combined.

1991 and 36–45 mm (length class 4) by the following spring (September 1991) at all sites (Fig. 4).

The length-weight relationships for fish collected from Noonameena, Policemans Point and Tea Tree Crossing are shown in Table 1. Statistical comparisons of the slopes by ANCOVA revealed non-significant differences between the sites in December 1990 and March 1991 (Tukey HSD, $p > 0.05$). In October 1990, significant differences were found between each of the three sites (Tukey HSD, $p < 0.05$), however the assumption of homogeneity of slopes was violated in this month ($F = 5.66$, d.f. = 271, $p = 0.004$). The slopes of the regressions, which indicate relative

weights and thus may be interpreted as a "condition factor", showed no consistent relationship with the salinity of the sites (Table 1).

The length frequencies of male and female fish in the trap and seine samples from all sites combined taken in October 1990, December 1990, March 1991 and May 1991 are shown in Fig. 5. Females were significantly larger than males (independent t-tests, $P < 0.05$) in each month. The largest female fish caught in the trap samples was 85 mm (November 1990) while males were below 67 mm (although a single male fish of 75 mm was collected in May 1991). Sex ratios (fish caught in the seine-net only) usually favoured females with significantly more females for all months combined ($\chi^2 = 37.82$, $N = 413$, $P < 0.01$). Orange coloration of the eyes and mid-lateral line was only

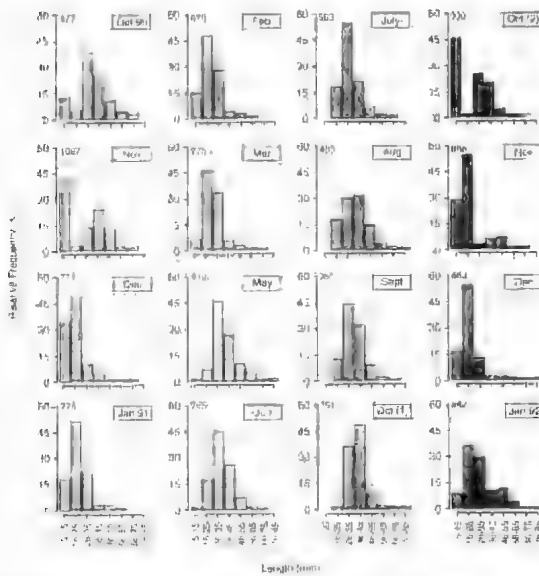


Fig. 4 Relative length-class frequencies of *Atherinosoma microstoma* caught in seine net hauls from October 1990 until January 1992 (two samples 14 days apart were taken in October 1991). Catches from the five sample sites have been pooled as there were no consistent differences between sites in length-class frequencies. The number of fish measured in each sample is indicated at the top left of each distribution.

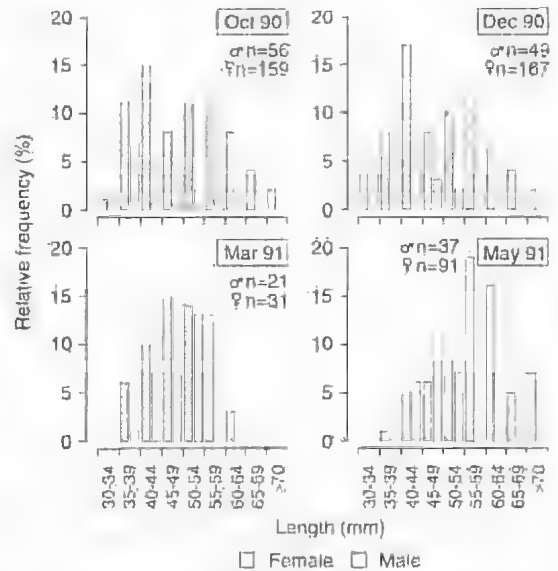


Fig. 5 Relative length-class frequencies for female and male *Atherinosoma microstoma* in October 1990, December 1990, March 1991 and May 1991. For each month fish from trap and seine-net samples were combined.

TABLE 1. Length weight regressions of *Atherinosoma microstoma* from Noonameena (NM), Policemans Point (PP) and Tea Tree Crossing (TTC) in October 1990, December 1990 and March 1991. Regressions are of the form $Y = ax^b$ where: Y = weight, X = length, a = intercept and b = slope. r^2 = coefficient of determination, n = sample size and *** = $P < 0.001$

Sample date	Site	a	b	r^2	n
October 1990	NM	9.12×10^{-6}	2.97	0.972***	69
	PP	1.55×10^{-5}	2.79	0.978***	125
	TTC	3.54×10^{-6}	3.12	0.891***	83
December 1990	NM	4.36×10^{-6}	3.12	0.975***	100
	PP	5.75×10^{-6}	3.04	0.969***	100
	TTC	8.13×10^{-6}	2.96	0.966***	100
March 1991	NM	6.03×10^{-6}	3.03	0.934***	100
	PP	8.32×10^{-6}	2.94	0.977***	100
	TTC	7.08×10^{-6}	2.98	0.961***	97

found in male fish over 36 mm TL and only during the breeding season (September-January), indicating that it is related to reproductive behaviour.

The relationship between total length (TL) and standard length (SL) was expressed by the following equation:

$$SL(mm) = 0.61 + 0.85 TL(mm) \\ (r^2 = 0.99, N = 34, P < 0.001).$$

Annual Reproductive Cycle of Atherinosoma microstoma in the Coorong

Only one ovary developed in female *A. microstoma* and this remained small (<2% of body weight or GSI < 2) through autumn and winter in the Coorong (Fig. 6). In spring, the ovaries showed a marked increase in size before declining over summer with similar seasonal patterns occurring at all sites (Fig. 6). The GSIs were highest during September and October in 1991. This annual cycle in reproduction was also reflected in the proportion of immature, mature, ripe

and spent fish in the samples (Fig. 7). Female fish possessed only immature oocytes from May to July. Maturing oocytes were first detected in August with large numbers of mature and ripe fish present throughout spring. Spent fish were first detected in November. Some immature eggs remained in the ovary indicating that not all oocytes were matured and shed

Batch Fecundity of Atherinosoma microstoma in the Coorong

The numbers of oocytes, classified as immature, maturing or ripe in the ovary of individual fish collected from the two breeding seasons are shown in Fig. 8. The large variation in numbers of immature oocytes may relate to fish size and to losses due to maturation. There were smaller numbers of maturing and ripe oocytes with most fish having from 5 to 40 maturing oocytes and 5 to 30 ripe eggs in the ovaries.

Batch fecundity (numbers of maturing oocytes) was strongly correlated with ovary-free body weight ($r^2 = 0.68, n = 101$) in spring 1991 at the time of peak gonad weight (Fig. 9a). Relative batch fecundity (numbers of maturing eggs per gram of ovary free body weight) for fish was independent of ovary free body weight ($r^2 = 0.04, n = 101$) (Fig. 9b), indicating that

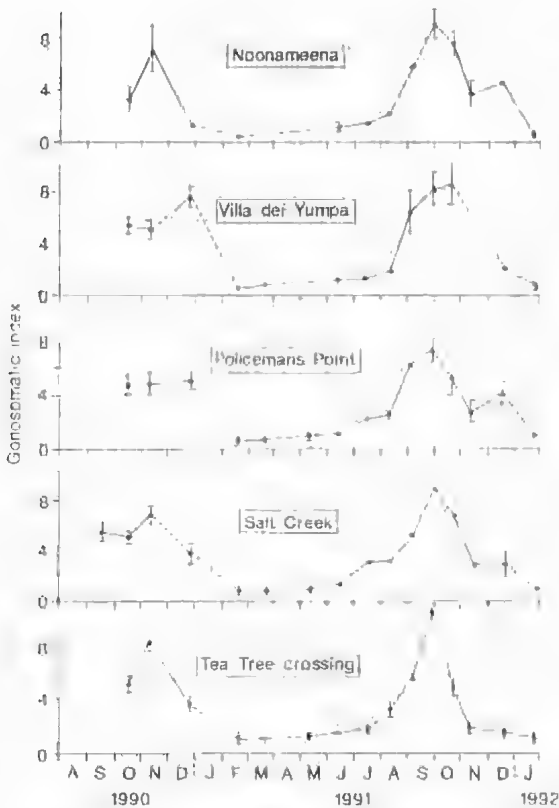


Fig. 6. Seasonal changes in the gonosomatic index of female *Atherinosoma microstoma* at five sites in the Coorong Lagoon. Points represent mean values of up to 20 fish and vertical lines are one standard deviation each side of the mean. No standard deviation is given when sample size was less than 10.

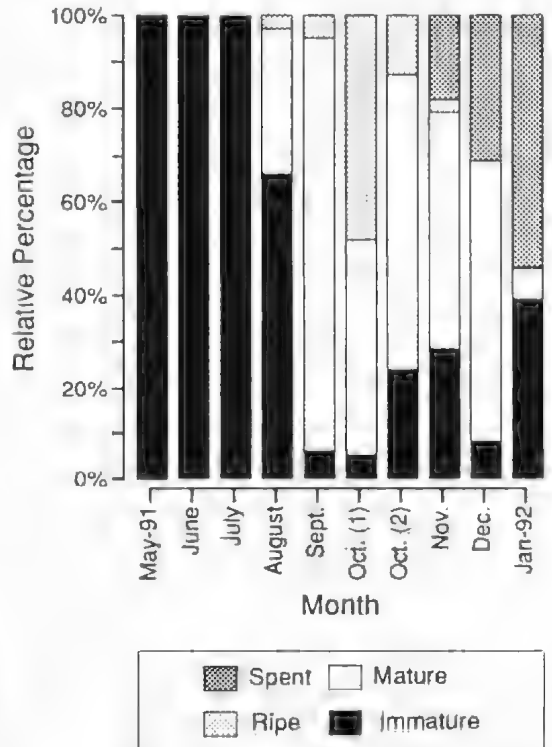


Fig. 7. Relative proportion of female *Atherinosoma microstoma* characterised by the most advanced clutch present in the ovary. Data from all five sites combined.

fish of different sizes were allocating a similar proportion of their resources to egg maturation. Relative batch fecundities (Fig. 10) were not significantly different between sites in spring 1990 ($F = 0.16$, d.f. = 2,45, $P = 0.851$) or 1991 ($F = 3.23$, d.f. = 2,98, $P > 0.05$). However, significant differences were found between years, with relative batch fecundities in 1990 being about half those of 1991 ($F = 51.67$, d.f. = 1,147, $P = 0.001$). The number of maturing eggs per ovary tended to decline after the peak spawning period in October 1991.

Discussion

Influence of Salinity on Distribution, Growth, Size and Condition of *Atherinosoma microstoma*

Over the summers of 1990-1991 and 1991-1992 the distribution of *Atherinosoma microstoma* in the Coorong was not restricted by salinity. All other fish species appeared to be limited by salinity during the high-salinity summer season in a manner similar to that reported in Geddes (1987) and Geddes & Hall (1990). The highest salinity at which *A. microstoma* was collected was 94 g L⁻¹. This record exceeds the maximum field salinity for this species from coastal salt ponds in Victoria (82 p.p.t., Chessman & Williams 1974). In March 1985, a few individuals of *A. microstoma* were trapped at 149 p.p.t. TDS (salinity approximately 130 g L⁻¹) at Tea Tree Crossing in the Coorong (Geddes 1987; D. C. Paton unpublished). *A. microstoma* ranks along with *Cyprinodon variegatus*,

which has been recorded at 142 p.p.t. TDS (Simpson & Gunter 1956), as one of the most salt-tolerant fish species in the world. This ability allows *A. microstoma* to survive at the southern end of the Coorong during extreme hypersaline conditions. Abundance data suggested that hardyhead numbers at the southern sites

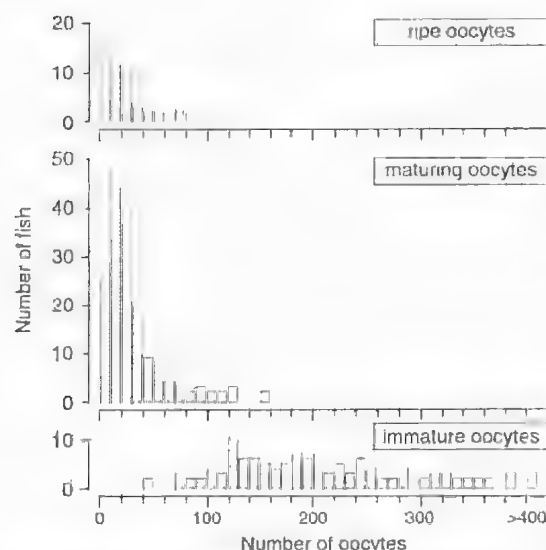


Fig. 8. Frequency distributions of the numbers of immature, maturing and ripe oocytes in the ovaries of female *Atherinosoma microstoma* caught in the Coorong during the 1990 and 1991 breeding seasons.

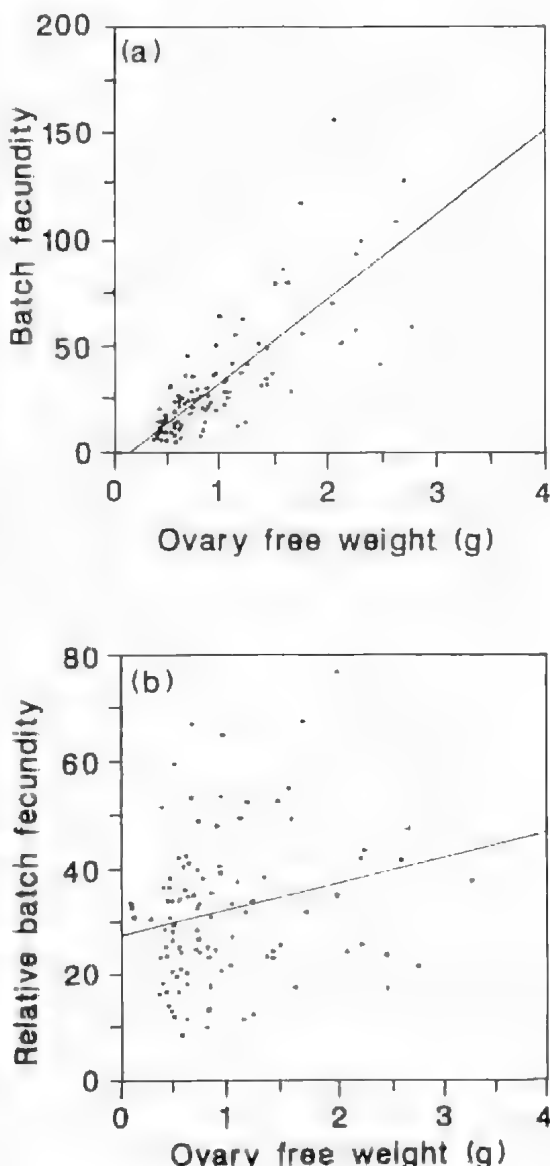


Fig. 9. Relationships between (a) batch fecundity and ovary free body weight ($r^2 = 0.68$, $n = 101$) and (b) relative batch fecundity and ovary free body weight ($r^2 = 0.04$, $n = 101$) for female *Atherinosoma microstoma*. Points represent fish collected in September, October and November 1991.

were not affected, but high variability, perhaps associated with schooling behaviour of the fish, and low numbers of samples were confounding factors in this analysis.

No major differences were found between sites in growth, size or condition of hardyheads in the Coorong. Growth rates implied from the progression of length modes suggest that *A. microstoma* can achieve a total length of 35 mm in four months, followed by a period of little growth over winter, reaching lengths of 45 mm the following spring, and thereby becoming sexually mature within the first year of life. There was no indication of dwarfism related to high salinity in this population. Maximum sizes for both sexes were similar at all sites in the Coorong and comparable to those found in the Dee Why Lagoon population (Potter *et al.* 1986) and for this species in general (Cadwallader & Backhouse 1983). Maximum total lengths recorded for males were 67 mm (present study) and 66.5 mm (Dee Why Lagoon) and for females 85 mm (present study) and 86.4 mm (Dee Why Lagoon). Fish condition in the Coorong did not differ significantly between sites in March when salinities were high and ranged from 58 at Nooameena to 92 g L⁻¹ at Tea Tree Crossing.

Life History, Annual Cycle and Population Structure of *Atherinosoma microstoma*

The post-breeding decline in larger fish at all sites from December indicates a one-year life cycle. The population showed a numerical dominance of females, and males were also significantly smaller than females. Similar patterns of life history and sexual dimorphism

have been found in the population at Dee Why Lagoon, New South Wales (Potter *et al.* 1986) and in atherinids from the Northern Hemisphere (e.g. Gon & Ben-Tuvia 1983). The proportion of female fish in this population appears to decline over the breeding season and a sex ratio of close to one is reached in December. This may be due to differential mortality during the breeding season, or to an increase in the numbers of male fish reaching maturity (>30 mm) as the season progressed. The orange coloration found in male fish appears to be related to reproductive activity and may be under hormonal control.

The marked difference in size between sexes, the prolonged breeding season and the short life cycle of *A. microstoma* may be indicative of a species where sex is determined after conception by environmental factors, such as temperature (Conover 1984). Conover & Kynard (1981) conclusively showed that temperature exerted a direct influence on primary sex differentiation, rather than causing sex specific mortality in the atherinid, *Menidia menidia*. Thus, if eggs spawned in the cooler spring waters develop into females, and eggs spawned in the warmer waters of late summer develop into males, then females would have a longer growing season which would account for their significantly larger size.

Spawning occurred from September to December giving a protracted four month spawning season. This is supported by the large numbers of larvae collected from October to December from all sites. The absence of larvae in the samples, the small GSIs, and the absence of maturing and ripe oocytes in the ovaries during autumn and winter 1991, indicates that this

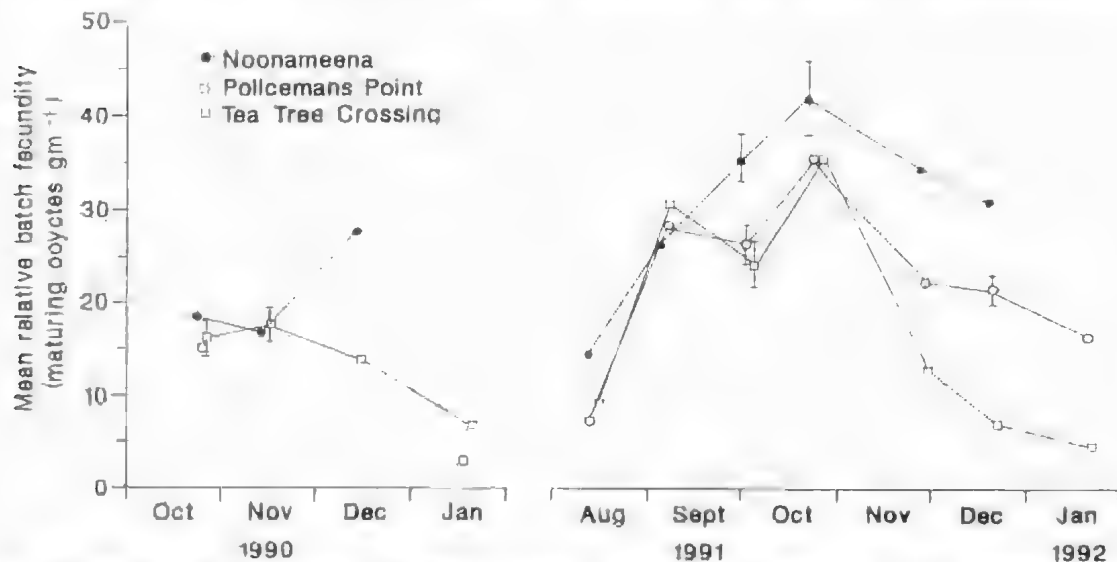


Fig. 10. Mean relative batch fecundity of female *Atherinosoma microstoma* from three sites in the Coorong Lagoon over the 1990-91 and 1991-92 breeding seasons. Points represent mean values of up to 20 fish and vertical lines are one standard deviation each side of the mean. No standard deviation is given when the sample size was less than 10. Only fish with maturing or ripe oocytes were included in the analysis.

species has only one breeding season per year. Mean gonosomatic indices and relative hatch fecundities were greatest in November in 1990 and October in 1991, indicating that spawning probably peaked during these months. The later onset of spawning in 1990 is reflected by the later drop in salinities in that year. Thus a reduction in salinity may be one of the environmental variables involved in triggering spawning.

A protracted spawning season may reflect repeated "batches" of eggs being spawned or a lack of population synchrony in gonadal development (DeVlaming 1983). Analysis of egg types shows that oocyte development in *A. microstoma* is "group-synchronous", as at least two size groups of oocytes were present in the ovary of an individual at some time during the reproductive cycle (DeVlaming 1983). This type of oocyte development implies that the whole clutch of ripe oocytes will be shed over a short period (West 1990). Multimodal frequency distributions of oocyte diameters, as found for *A. microstoma* in the Coorong, are characteristic of multiple-spawning fishes (Hempel 1979). The presence of several modes of developing oocytes, the presence of remnant ripe eggs in some ovaries and the decline in the number of maturing eggs per fish as the spawning season progressed indicates that *A. microstoma* is a multiple-spawning fish. Multiple batches of eggs spawned successively within one spawning period have been found in other atherinids including *Menidia menidia* (Conover 1984) and *M. audens* (Hubbs 1976). Protracted spawning is common among atherinids in Australia (e.g. Ivantsoff 1978; Prince & Potter 1983; Potter *et al.* 1986) and in the Northern Hemisphere (e.g. Carpelan 1955; Gön & Ben-Tuvia 1983; Conover 1984; Middaugh & Hemmer 1992). A four month protracted breeding season over spring parallels that found for this species from Dee Why Lagoon, New South Wales, where spawning occurred from August to November (Potter *et al.* 1986).

Influence of Salinity on the Reproductive Performance of Atherinosoma microstoma

A. microstoma is the only recorded Australian atherinid to reproduce in hypersaline waters, with the possible exception of *Craterocephalus pauciradiatus* (Lenanton 1977). The gradient in salinities along the Coorong did not reduce the length of the spawning season in *A. microstoma* as fish were in spawning condition from September to December in both 1990 and 1991 at all sites. Salinities during these periods ranged from 32 g L⁻¹ at Noonameena in September 1990 to 74 g L⁻¹ at Tea Tree Crossing in December 1990. Salinities are usually at their lowest in the Coorong during spring which may account for the lack of any clear influence of salinity on reproduction in the present study.

Gonad development commences in late winter/early spring at a time when day length and temperature are increasing and these are likely to be the environmental cues for gonad recrudescence. Breeding in spring may be timed to take advantage of seasonal peaks in food availability. In the Coorong, hardyheads feed mainly on zooplankton, in particular ostracods and copepods, and these are most abundant during winter and spring in the Coorong when salinities are relatively low (Geddes 1987). Female hardyheads only develop a portion of their eggs at one time, suggesting that either a physiological or ecological factor (e.g. insufficient food) limits hatch fecundity. Relative hatch fecundities and gonosomatic indices were lower in 1990 when the growth and performance of *Ruppia tuberosa*, a key aquatic plant in the southern Coorong, was reduced compared with 1991. Other resources including zooplankton may also have been lower. Multiple spawning is a common reproductive strategy among small fish species and maximises the numbers of eggs a small fish can produce (Potter pers. comm.). In addition, *A. microstoma* may be able to adjust batch size in response to environmental conditions. Such a strategy would allow hardyheads to exploit both longer reproductive seasons and better quality seasons. This strategy would require the initiation of more oocytes than would be expected to be shed in most years.

The Role of Atherinosoma microstoma in the Coorong

Atherinids are an important component of the biomass of small fish of many aquatic ecosystems, including Bandawil Lagoon (Ben-Tuvia 1984), Laguna Madre (Hedgpeth 1967), Hamelin Pool (Lenanton 1977), Peel Harvey estuary (Potter *et al.* 1983) and the Swan-Avon River system (Prince & Potter 1983). *A. microstoma* is a prominent component of the Coorong ecosystem, in particular as a major food item for selected piscivorous water birds (Paton 1982). High and fluctuating salinities along the Coorong did not have a marked effect on the population ecology or reproductive behaviour of *A. microstoma* and no significant differences in relative hatch fecundities were found between sites that differed in salinity within a year. Thus, *A. microstoma* appears to be well adapted to hypersaline conditions and future small changes in salinity would not be expected to affect hardyheads in the Coorong. However, their food supply may be affected by salinity. Future studies should be directed toward the diet of *A. microstoma* in the Coorong and the factors that might limit these resources.

The agricultural areas of the Upper South East of South Australia suffer from dryland salinization and seasonal inundation of lowlying areas with surplus surface water. There are proposals to drain some of this surface water and possibly groundwater into the South Lagoon of the Coorong (Upper South East Dryland Salinity and Flood Management Plan Steering

Committee, 1993¹). Such inputs of fresh or brackish water may disrupt the seasonal fluctuations in salinity which are an important feature of the Coorong and which may act as a partial cue to spawning in *4. microstoma*. Other consequences of the inputs, such as an increase in water depth and consequent reduction in the exposure of the highly productive mud flats, or a rise in nutrient or heavy metal concentrations may also affect the food chains in the Coorong supporting *4. microstoma* and in-turn piscivorous birds. Consideration needs to be given to the role of hardyheads in the Coorong ecosystem in future management proposals.

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¹ Upper South-East Dryland Salinity and Flood Management Plan Steering Committee (1993) Upper South-East Dryland Salinity and Flood Management Plan: Draft Environmental Impact Statement. Natural Resources Council of South Australia.

REDESCRIPTION AND ECOLOGICAL NOTES ON THE PYGMY BLUETONGUE, *TILIQUA ADELAIDENSIS* (SQUAMATA: SCINCIDAE)

BY *MARK N. HUTCHINSON**, *TIM MILNE†* & *TIM CROFT‡*

Summary

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A preliminary study of a population of the pygmy bluetongue, *Tiliqua adelaidensis* (Peters, 1863) has enabled us to redescribe the species and give a preliminary account of its natural history. Life colouring, intrapopulation variation, sexual dimorphism and general morphology of the skull and mandible are described. Pygmy bluetongues at the study site are diurnal inhabitants of open tussock grassland and use spider holes for shelter. Males had enlarged turgid testes during spring and a female examined at this time had yolked ovarian follicles. Males were more active and trappable than females during spring, but both sexes were sedentary during late summer-autumn. Litters of 1-4 live young were born in the maternal burrow during February-March. We suggest that the lack of sightings of *T. adelaidensis* this century has been due partly to its specialised ecology and partly to a real decline attributable to habitat destruction.

Key Words: *Tiliqua*, Scincidae, lizards, morphology, natural history, conservation.

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KEY WORDS: *Tiliqua*, Scincidae, lizards, morphology, natural history, conservation.

Introduction

"kommt nur auf sandigem, steinigem terrain vor"
(Richard Schomburgk, quoted by Peters, 1863)

Schomburgk's remark ("found only in sandy, stony terrain") is the only published first-hand information available on the ecology of *Tiliqua adelaidensis*, the pygmy bluetongue lizard, a species which has been regarded as one of the most seriously endangered of Australia's reptile species, if not actually extinct (Cogger 1992; Ehmann 1992; Hutchinson 1992). The discovery of a population of the species near Burra, S.A. (Armstrong & Reid 1993; Armstrong *et al.* 1993), following the first sighting of the species for 33 years, has presented an opportunity for urgently needed study of the species which had previously been known from only 20 museum specimens, mostly collected last century (Ehmann 1982; Shea 1992).

The original description (Peters 1863) was brief, based on two syntypes probably collected in the vicinity of Gawler, S.A. Mitchell (1950) redescribed the species based on SA Museum specimens and figured the head shields and whole animal for the first time. No further formal descriptions have appeared in print, save for those of Cogger (e.g. 1975, 1992), based on the old

and faded museum material. Shea (1990) described a number of scalation and osteological character states for *T. adelaidensis* in order to establish the validity of the genera *Tiliqua* and *Cyclodomorphus*. Shea's unpublished thesis (1992¹) gives a thorough description of the species' scalation, morphometrics, colour pattern and osteology based on the twenty specimens then extant. Shea & Hutchinson (1992) illustrated and commented on the dentary and dentition of *T. adelaidensis*.

Ehmann (1982) summarised available data on diet and external morphology and drew together the meagre data bearing on the provenance of the specimens known to him. He also attempted to reconstruct the species' ecology, using analogies with related or physically similar reptile species. These speculations were cited several times subsequently, sometimes in such a way that it was not clear that there were no direct observational data on the subject (Ehmann 1992).

Field work has begun, aimed at determining the best methods for locating *T. adelaidensis*, gathering preliminary data on its ecology and making a first attempt to determine the number and size of surviving populations. This article gives a summary of the morphological variation that we have observed within a single population of *T. adelaidensis* and provides a preliminary account of its natural history at this site.

Methods

Current research on the biology and conservation of this species is concentrated on one site located in the Burra area (33°41'S, 138°56'E), approximately 160 km north of Adelaide, South Australia. The site was the first of several found to support *T. adelaidensis*, following the initiation of fieldwork in October, 1992

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¹ SIMA, G. M. (1992) The systematics and reproduction of bluetongue lizards of the genus *Tiliqua* (Squamata: Scincidae). Unpub. PhD thesis, Dept of Veterinary Anatomy, University of Sydney.

(Armstrong *et al.* 1993). The data presented here stem from the first season of field work on this population, carried out from mid-October 1992 to mid-May, 1993.

Specimen Collection

Live *P. adelaidensis* were collected by three methods.

Pitfall traps, 30 metre stretches of fly wire drift fencing were erected, along which were placed six 25 cm lengths of PVC pipe dug vertically into the ground. Four traplines were set at the study site during the period 4 November–20 December, 1992. An additional line was in place during 30 November–20 December and a further two were set on 4 December. The five most successful spring traplines were reset during 2–21 February 1993. Total trap nights by this method were 1,956.

The other two methods relied on the species' hole-dwelling habits (see *Habitat* section).

Hand collection. This method relied on opportunistic sightings of free ranging animals, or on surprising animals at the entrances to burrows. Most individuals caught by hand were juveniles which were extracted from burrow entrances using long forceps or clamps.

We also used a method we termed 'fishing', enticing lizards to seize an insect bait tied to a cotton thread. A grasshopper on a piece of cotton tied to the end of a three metre bamboo pole was held outside the entrance of the lizard's burrow; lizards seizing the grasshopper could be pulled into the air and captured as they dropped to the ground and tried to return to the burrow (Strong *et al.* 1993 describe a similar collection technique). Lizards had to be lured completely out of the burrow before being allowed to seize the grasshopper, since the lizard's hind limbs could hold the burrow rim, preventing its dislodgement. Their extreme wariness made the use of a long pole necessary to distance the collector from the lizard.

Trapping using baited (peanut butter or sardines) aluminium 'Sherman' traps was tried but without success (approximately 2,500 trap-nights).

The time of day of collection was noted, as was the daily maximum temperature. Lizards were measured and sex was determined by the presence of bulges at the base of the tail and/or hemipenes in males, with a lack of these features indicating a female. The lizards were then marked by toe clipping, photographed and released. Only one or two toes were removed, this limited number in conjunction with colour pattern variations being sufficient to identify each individual.

A limited use was made of radiotracking using a small external unit supplied by Transceiver Services, Adelaide, attached using superglue and surgical tape to the lizard's shoulder. The device was intended for short term use, and was run successfully on a single lizard, located every two hours, for six days. A second

trial resulted in the death of the lizard within the first two-hour period and use of this approach was discontinued.

In the descriptive section, scale features occurring bilaterally were counted on both sides. Paravertebral scales were counted using Greer's (1982) method.

Vegetation was quantitatively assessed around the most successful pitfall line using two methods:

a) We recorded all plant species in a 30 m × 30 m quadrat, 15 m either side of each pitfall line, taking collections of plants in cases where identity was not clear. These collections were subsequently identified and lodged with the State Herbarium.

b) We assessed vegetative cover within the 30 m × 30 m quadrats by the simple transect method known as 'Step-point' (Cunningham 1975). At every step in set directions across the quadrat we recorded the plant species encountered at the tip of the shoe, scoring approximately 300 points in the quadrat. This method gives estimates of percentage of ground cover of plant species, bare ground, rock and litter.

The behavioural data we present stem mainly from field observations, but we obtained confirmatory data in many cases from observations of captive specimens at Adelaide Zoo (T. Morley and R. Ainsley pers. comm.).

Description

Specimens

The following descriptive section is intended to show variation within a single population. Earlier authors (Ehmann 1983; Mitchell 1950) give additional data from some of the older specimens, and all of the available data on this older material is discussed in Shea's thesis.

A total of 63 specimens was collected during the survey period, and an additional four were born in captivity. Six of these specimens were collected dead, killed by the elapid snake *Pseudonaja textilis* (four specimens) or birds of prey (two specimens). A seventh, R40838, died during trials of an external radio transmitter. Four specimens, an immature, an adult male and two adult females, were retained and are on loan to Adelaide Zoo. The remainder were marked and released. The success of collection methods varied according to time of year. Pitfall trapping was successful only during November–December, while hand collection became much more successful in February–April (Table 1).

All predator-killed specimens are damaged, although in two the damage was minor and confined to restricted areas of the body. R40687 and R40744 had some necrotic patches on the dorsal and ventral body surface. R40687 had a sagittal fracture of the skull running from the nasal scale to the level of the eye. R40689 had the left neck and posterolateral region of the skull deeply gouged and partly removed and a deep

wound in the right side of the neck, R40728 lacked the head and right forelimb, as well as the liver, heart, lungs and stomach, R40738 and R40745 were partly digested, with the skin on the body sloughing away and much of the internal soft anatomy missing. Two skulls and associated mandibles were prepared from snake-killed specimens, one articulated (SAMA R40738) and one partly disarticulated (R40745).

TABLE 1. Relative success of capture techniques.

Method	Number caught	
	November-December	February-May
Pitfalls	17	nil
Hand	5	21*
"Fishing"	not used	14

* All but one neonates

General Appearance

Tiliqua adelaidensis is a moderate sized skink with short extremities, a relatively heavy body and large head. The body and tail are soft and flexible, but the head is heavily armoured by the well developed head shield osteoderms. The toes are short, the third and fourth toes of the hind foot being equal in length. The tail tapers rapidly from the base and is thin and slightly laterally compressed over the distal two-thirds.

Colour

The dorsal surface of the head, body, limbs and tail is light grey brown, yellowish brown, orange, tan or chocolate brown, the distal portions of the extremities, especially the forelimbs, being a paler yellowish hue. Dorsal and lateral scales usually have narrow darker edges producing fine, longitudinal lines along the back and sides. The lower lateral surfaces are pale greyish becoming off-white ventrally. The dorsal surface is unmarked, or shows variable development of blackish spotting, including a vertebral series of irregular small blotches (which may coalesce into a ragged vertebral stripe) from the nape to the base of the tail, and several laterodorsal and upper lateral series of small black flecks; these may be crudely aligned to form weak transverse bars. The midlateral region often has scattered grey-white flecks. The venter is immaculate, or with slightly greyer margins to the scales forming narrow longitudinal lines. The iris of the eye is bright orange. The tongue is pale rose pink, with no trace of melanic pigmentation. The roof of the mouth and buccal commissures are mauve. The abdominal peritoneum is black. Juveniles are consistently greenish grey to mid-brown, becoming reddish tan on the tail and limbs. The range of variation in black pigmentation is similar to that seen in adults, but many juveniles have more extensive and obvious white spotting on the body.

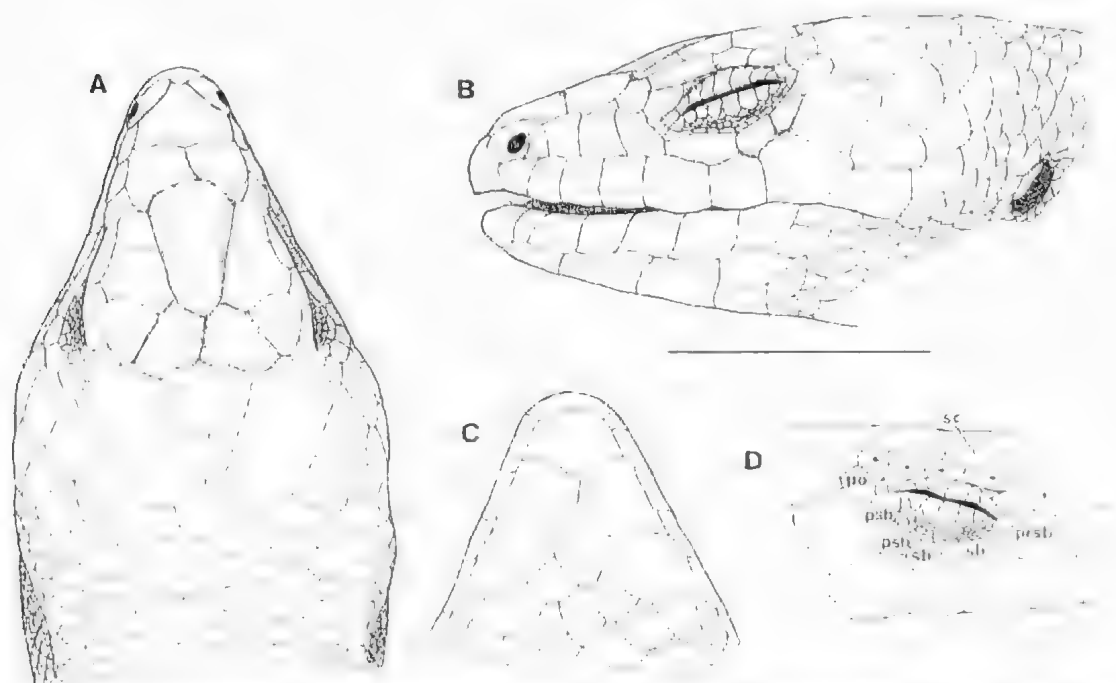
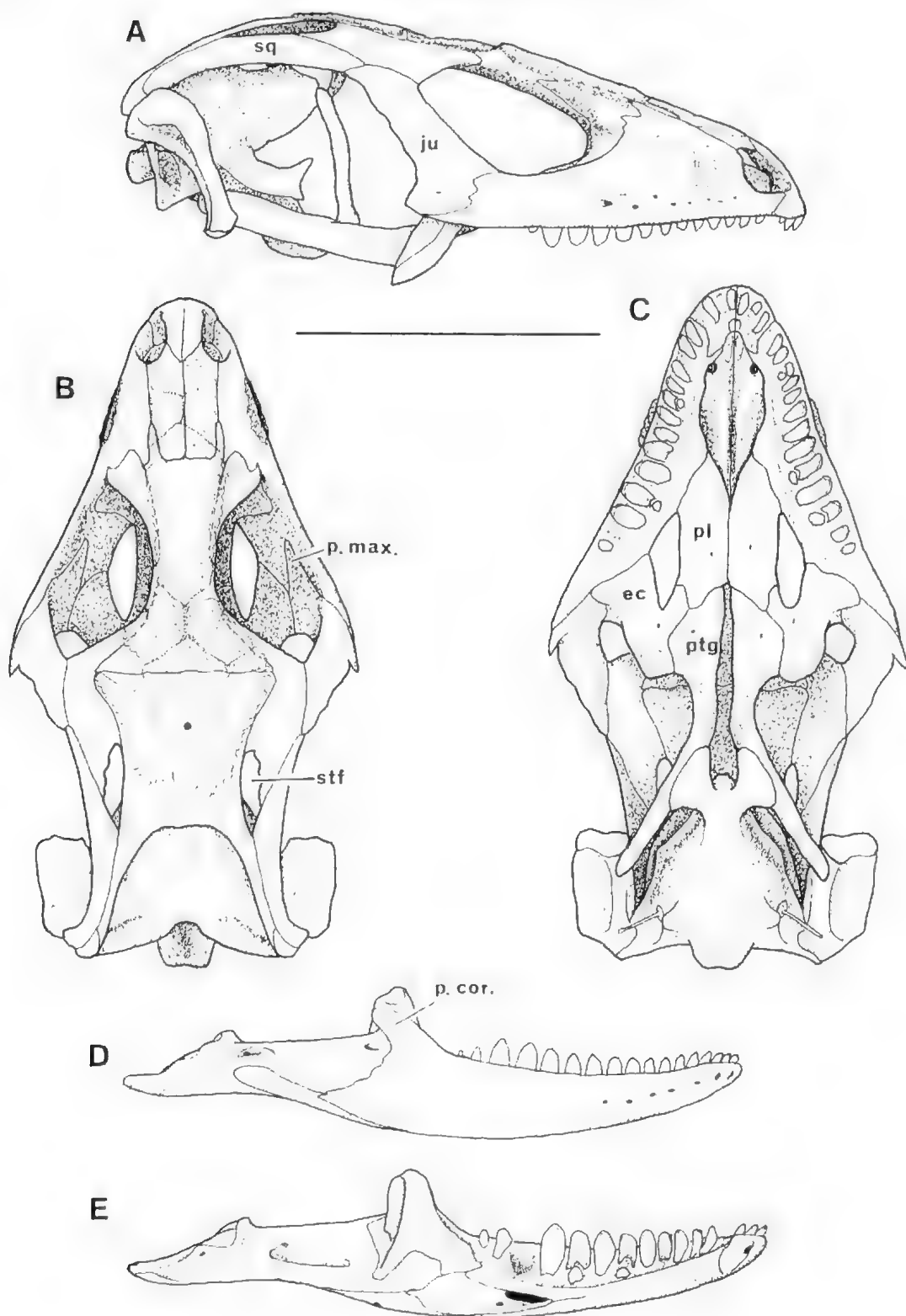


Fig. 1. Head shields of *Tiliqua adelaidensis* (SAMA R40838). A, dorsal view. B, left lateral view. C, detail of chin shields. D, detail of right side showing asymmetric variation in circumocular scalation. Abbreviations for circumocular scales: po, postocular; psb, presubocular; psh, postsubocular; sh, subocular; sc, supraciliaries. Scale bar = 10 mm.



Scalation

This is based on eight specimens, four held in the S.A. Museum (R40687, R40689, R40744 and R40838), plus a live adult male, two adult females and subadult held at Adelaide Zoo. The head shields are shown in Fig. 1.

The species has the scalation characteristics listed by Shea (1990) for *Tiliqua*. The last supralabial is horizontally divided, and the temporal scalation posterior to the secondary temporals is irregular and little differentiated from the body scalation. The supraciliary scale count is reduced (mode 5). A complete subocular scale row, consisting of a large presubocular, a larger anterior and smaller posterior subocular and one or two postsuboculars, runs from the anterior supraciliary to the postocular. Nuchals are absent or a single slightly enlarged pair may be present, often separated by a median occipital or internuchal scale.

Dorsal scales smooth, in 33–36 (mean 34.6) rows at midbody; paravertebral scales 77–86 (mean 83.0); paravertebral scales between parietal and the level of anterior edge of hind limb 70–81 (mean 77.6); subdigital lamellae under fourth toe unpaired, 10–13 (mean 11.6); nasals in point contact or narrowly separated (0.2); strong postnasal groove present; prefrontals in broad contact; frontoparietals paired; interparietal about same size as frontal, much larger than frontoparietals and separating parietals; each parietal in contact anterolaterally with the postocular and posterior supraciliary and bordered posterolaterally by four or five enlarged scales; a median occipital scale present or absent (0.4) posterior to interparietal; supraoculars 3/3, the first two contacting the frontal; supraciliaries 5/5 (5/6 in one specimen), the second the longest; complete subocular scale row present; supralabials 8, the eighth only half as high as the seventh; infralabials 7–9 (mean 7.9); a single primary temporal is followed by three secondary temporals; postmental contact first two infralabials; a single large, quadrangular anterior ear lobule.

The dorsal head shields, frontonasal, prefrontals, frontal, frontoparietals and interparietal, are thickened, with weakly corrugated surfaces and deeply incised sutures. This rugosity increases with size. In large males the subocular scales also become thickened and slightly overhang the suborbital supralabials.

Skull and mandible

The characteristics noted for the species by Shea (1990; 1992¹) are confirmed in the SAMA specimens. The species has moderately narrow separation of the pre- and postfrontals on the medial orbital margin. Finger-like nasal processes of the frontals are present to give a W-shaped frontal-nasal contact. The jugal is broad and flattened and contacts the postfrontal. A lacrimal bone is absent. There is a well-developed medial palatine process of the ectopterygoid which excludes the pterygoid from the edge of the infraorbital vacuity. The coronoid process of the dentary is enlarged and swept back to cover the lateral face of the dorsal process of the coronoid. Dentition is heterodont, with the cheek teeth markedly larger than the anterior teeth.

In general aspect (Fig. 2), the skull and mandible of *T. adelaidensis* are very like those of other *Tiliqua* species. The proportions of the snout, tapering and pointed, rather than blunt and rounded, and the parietal region, constricted, rather than laterally expanded, resemble those of adults of the other species of *Tiliqua*. The dorsal head shield osteoderms are intimately fused with the bones of the skull roof, to a greater degree than is usual in most other *Tiliqua*. Thus, even though *T. adelaidensis* is as small as or smaller than congeneric neonates, it is ontogenetically advanced in its proportions and degree of ossification. In these features *T. adelaidensis* is progenetic, not neotenic as is frequently the case in miniaturised lizards (Rieppel 1984). Even so, *T. adelaidensis* also shows some neotenic features in retaining relatively large upper temporal fenestrae and in some aspects of braincase anatomy (Shea pers. comm.).

Unique or unusual features of the skull are few but include the very closely apposed, almost parallel palatal rami of the pterygoids. In most other *Tiliqua* (*T. gigas* is an exception) the pterygoid margins are more widely separated and diverging. The closely apposed pterygoids may be correlated with a narrowing of the skull posteriorly as *T. adelaidensis* has the greatest skull width across the jugals, rather than at the level of the quadrates. The maxillary process of the jugal tapers rapidly and fails to contact the prefrontal. This character state is shared with *T. multifasciata* and most *T. orchipeltis*, whereas other *Tiliqua* species have the jugal extending anteriorly to contact the prefrontal adjacent to the lacrimal foramen.

Fig. 2. Skull and mandible of *Tiliqua adelaidensis* (SAMA R40738). A, skull, right lateral view, showing contact between jugal (ju) and squamosal (sq) bones. B, skull, dorsal view, showing short maxillary process of the jugal (p. max.) and open supratemporal fenestrae (stf). Note persistent head shield osteoderms which obscure sutures of prefrontal and postfrontal bones, other skull roof sutures are visible through the osteoderms. C, ventral view, showing configuration of the palatal complex (ec, ectopterygoid; pl, palatine; pig, pterygoid). D, right mandibular ramus, labial view, showing very well developed coronoid process of the dentary (p. cor.). E, left mandibular ramus, lingual view. Scale bar = 10 mm.

The upper temporal fenestrae are relatively larger than in adults of other *Tiliqua* species, in which they are slit-like or absent.

Dimensions

Based on 61 specimens. Snout-vent length (SVL) 38–107 mm (mean 73.2). Axilla-groin length (AGL) 23–67 mm (mean 44.0, $n = 58$). Snout-axilla distance (SAD) 16–41 mm (mean 28.3, $n = 58$). Forelimb length 11–21 mm. Hind limb length 11–21 mm. Tail length (TL) 22–79 mm.

Sexual Dimorphism

Adult males and females (arbitrarily defined as >85 mm SVL) differ markedly in head and body proportions. Adult males on average are shorter than females (SVL males range 87–106, mean 93.4, $n = 17$; females range 88–107, mean 98.3, $n = 14$) but head size does not overlap (SAD/SVL males 0.36–0.42, mean 0.38, $n = 17$; females 0.30–0.35, mean 0.33, $n = 14$). The relatively large head size of males is a frequent phenomenon in skinks (e.g. Sunbwa 1985; Hutchinson *et al.* 1989; Hutchinson & Donnellan 1992) but is rarely as marked as it is in large adult male *T. adalaidensis*. Male combat has been recorded in other *Tiliqua* species (reviewed by Greer 1989), a selective pressure which might lead to their large head to body ratios.

Ecological Notes

Habitat

The main study site lies at an elevation of about 500 m on undulating terrain cut by small, intermittent stream courses. The ground is stony in places, with underlying shale and sandstone bedrock just exposed on the surface. The soil is hard-packing clay-sandy loam (red-brown earth, French *et al.* 1968). The vegetation of the main trap site is characteristic of degraded remnant native grassland, with the area around the site being bare of trees and shrubs (Table 2). A full list of plant species is provided in the Appendix. The exact original nature of this grassland is unclear, as copper mining and farming near the site

since 1845 may have resulted in the removal of trees and shrubs for both industrial and domestic use. Similar hilly areas in the district support *Allocasuarina verticillata* (drooping she-oak) low open woodland over similar ground cover of native grasses (*Stipa* spp., *Danthonia* spp.) and mat-rush or 'irongrass' (*Lomandra* spp.), as recorded in the survey area. Jessup (1948) concluded that at least some of the area had probably been essentially treeless prior to European settlement.

The relative abundance and species composition of native grass species varies within the study area. The immediate vicinity of the most productive trapline was dominated by one species of spear grass (*Stipa*, tentatively identified as *S. eremophila*), but elsewhere in the same paddock, pygmy bluetongues were found where *S. nodosa* was the common spear grass, and other grasses, notably wallaby grasses, *Danthonia* spp., and wire grass, *Aristida behriana*, were locally common. Thus the precise species composition of the understorey may be less important for the survival of pygmy bluetongues than the tussocky structure which provides ground cover throughout the year. Other areas surveyed in nearby paddocks which do not appear to support pygmy bluetongues showed increased ground cover by introduced plant species, and hence a decrease in the amount of cover during late summer-autumn. Even at the least disturbed part of the study site, only 50% of the ground cover is perennial vegetation, so that the surface of the ground is far more exposed in autumn than in spring. Adjacent areas that have been ploughed at any stage show minimal recolonisation by native plants, in particular *Lomandra* spp.

Aside from a single juvenile found under a stone, the only microhabitats in which *T. adalaidensis* have been found sheltering are vertical or near vertical holes. We suggest that the lizards are using spider holes, not digging their own burrows. The holes are perfectly circular, up to about 20 mm in diameter, lack any sign of excavated soil at the entrances and are indistinguishable from holes at the study site inhabited by lycosid and mygalomorph spiders. In at least one case a lizard inhabited a hole to which the lid of a trapdoor spider was still attached. Two large species of wolf spiders, *Lycosa stirlingi*, which makes a lid for its burrow, and *Lycosa gilberta*, which does not, have been identified at the study site as has a species of the trapdoor spider genus *Blakistonia* (probably *B. aurea*). Lycosids and their burrows are very common in the area. The lizards appear to make no obvious external modifications to the holes, save for a slight bevelling of the edges caused by their coming and going.

Home range and movements

We obtained few recaptures, and made only limited use of radio-tracking, so that our results are preliminary.

TABLE 2. Ground cover at *Tiliqua adalaidensis* study site (averaged over three quadrats).

		% Cover	No. Species
Vegetation			
Native	Annual	<1	1
	Perennial	22	32
Introduced	Annual	56	18
	Perennial	14	2
Bare Ground		3	
Rock		4	
Later		<1	

The area covered by a male that was radiotracked during spring encompassed 70 m² and two burrows over a period of six days. Home range overlap occurs, as there were at least two other occupied burrows within the area that the lizard covered. A second, smaller male was fitted with the tracker, but when relocated after the first two hour period it was moribund, apparently through exhaustion as it struggled to force itself into a hole but was prevented by the bulge of the transmitter. It was striking that, although shelter in the form of dense grass and *Lomandra* tussocks was all around, the lizard put all of its efforts into finding shelter in a hole.

The same male successfully tracked in November was caught again during March. It was still within the same area as the previous spring but in yet another hole. In another case, a burrow containing a female and young was abandoned and the female was discovered in another hole some 5 m from the original.

Only one of 22 captures during November–December was an adult female. All animals captured during spring/early summer were caught either by pitfall trapping or by hand, and so required the individual to be actively moving away from the burrow. However, of the adults captured during February–April one (a female) was captured by hand and 14 by “fishing” but pitfall trapping caught none, despite in excess of three weeks’ intensive pitfalling in areas known to support a significant number of pygmy bluetongues. Of the adults caught during summer/autumn, 12 were females, and three were males, a reversal of the trend shown in spring/early summer.

The top-sided sex ratio in our spring sample (only a single adult female caught) suggests much greater levels of male activity during the spring mating season. This is supported by the six predator kills collected during October–November, of which five were sexually mature males, while only one was an adult female. Males of other species of *Tiliqua* have increased activity levels relative to females during this time of year (Bull *et al.* 1991). The results so far indicate that both males and females may have relatively limited home ranges throughout most of the year, but in spring males appear to wander more widely (or at least, more often).

During November–December 1992, rainfall was above average and daily maxima ranged between 15°C and 36°C. Days when lizards were caught had maxima between 20°C and 36°C, and the time of capture varied from 08:15 to 19:30. All of the days on which pygmy bluetongues were caught were sunny at some stage, and so ground temperatures often would have exceeded the air temperatures. Traps were monitored after dusk on warm nights to check for nocturnal activity, but no lizards were captured at this time. Diurnal behaviour was also observed in captives, which showed no sign of nocturnal activity.

Diet

R40687 contained a large lepidopteran larva (a hadenine noctuid, probably *Persecutaria*, G. Brown pers. comm.); R40689 had the remains of an apparently identical larva, plus several leaves and flowers of the herb *Medicago*. R40744 contained three acridoid grasshoppers and the remains of a small beetle. Ehmann (1982), after examining specimens then in the SAMA collection, recorded cockroaches, ants, a spider, grasshopper and beetle, and some plants (*Dianella* seed, possible chenopod material). Wild lizards accepted grasshoppers offered as bait, and captive animals eat an omnivorous diet, including mealworms, crickets, chopped fruit and vegetables and raw egg. Thus the evidence to date indicates that *T. adalaidensis* eats a wide variety of invertebrate animals, but also includes plants in its diet.

The relative lack of movement away from the burrows, at least in late summer–autumn, suggests that at this time of year *T. adalaidensis* is probably a sit-and-wait forager. Burrow entrances are used as vantage points from which lizards would be able to make short forays after any prey detected nearby. The presence of leaves and flowers in the diet suggests wider foraging at least in spring. The study site suffered an outbreak of plague locusts (*Chortoicetes terminifera*) during the period of observation which may have influenced the lizards’ behaviour. The sedentary behaviour may also be related to avoiding predation at the time of year when ground cover is sparsest.

Reproduction

All of the predator killed males (collected between 14/10/92 and 30/11/92) had testes that were enlarged and turgid or starting to regress. One of the trapped males had strings of dried seminal material protruding from the vent. The single dead female (R40744, collected 7/11/92) had four enlarged ovarian follicles (two left, two right). Together these data indicate a spring testicular maximum, with spermiogenesis and mating behaviour coinciding with ovulation. Other *Tiliqua* species syntopic with *T. adalaidensis*, *T. rugosa* and *T. scincoides*, are known to be spring breeders (Bourne *et al.* 1986; Shea 1993).

Neonates were first observed at the field site on 28 February, 1993, when four young were observed in the burrow of an adult female. Inspection of other burrows known to harbour females revealed other litters, litter size ranging 1–4 (mean 2.3). All juveniles examined at this time had raw pink umbilical scars indicating very recent birth. Two females which gave birth at Adelaide Zoo during mid-March had litter sizes of three and one. Within two weeks of their discovery, juveniles and sometimes adults abandoned the birth burrow. Juveniles were observed from late March alone in holes, sometimes much smaller than those used by adults.

The smallest animals caught in November were 66–70 mm SVL, while the largest young with distinct

umbilical scars in May were 56–60 mm SVL. This implies that the *T. adelaidensis* born at the end of summer reach about 70 mm SVL by the end of spring of that year. This SVL is considerably smaller than the smallest breeding female recorded (SVL 96 mm), so that first breeding must occur no earlier than the second spring (approx. 20 months of age).

Behaviour

Tiliqua adelaidensis appears to be extremely sensitive to both movement and noise, making it difficult to observe lizards basking outside their burrows. Lizards bask with the back legs or tip of the tail remaining in the entrance of the burrow. From this position, they can back rapidly into their burrows if disturbed. Once inside, the lizards increase their security by turning the head sideways to force the snout and occiput against the sides of the burrow. Thus wedged in place, the lizards present only the armoured head to an intruder and seem almost invulnerable: any creature small enough to enter the hole is unlikely to be strong enough to harm or dislodge the lizard. The significance of the heavy osteodermal armour on the head seems to be associated with the use of the head as a combination anchor and doorstop.

Several behavioural attributes of captive lizards suggest why detection of the species in the field is difficult. The first is crypsis. When disturbed the lizards freeze: such stationary animals are well camouflaged against the reddish brown soil of the area, making them hard to see. The second is a reluctance to emerge into open spaces. In captive conditions the lizards spend almost all of their active time in holes or among litter. Thirdly, the lizards have a well-developed and unusual ability to move in confined spaces. Both in the field and in captivity they have been observed moving directly backwards into cover or down a burrow, avoiding a U-turn with its concomitant greater level of disturbance. The small, thin tails may facilitate this manoeuvre by not getting in the way as they might if longer or more massive. The body is unusually flexible, an attribute which probably assists in negotiating the confined spaces of burrows or tussocks. On several occasions, an animal was known to have entered a hole head first, turned around within the hole and emerged head first.

When disturbed or handled, this species has not yet been observed to exhibit the exaggerated defensive display employed by its larger relatives (Carpenter & Murphy 1978; Greer 1989). When handled the lizard will twist with great strength and agility, often gaping and endeavouring to bite in a similar fashion to other medium-sized skinks (e.g. *Egernia* spp.).

Possible Reasons for Decline

Tiliqua adelaidensis remained undetected in a well frequented part of South Australia for over three

decades in spite of diligent searching by herpetologists. Based on our experience with the species, we suggest that two factors combined to hamper searchers – lack of information on its habits and habitat, and a probable real decline in the number of populations.

Ehmann (1982), based on his interpretation of the specimens and historical data, speculated that *T. adelaidensis* had inhabited a limestone-chenopod-mallee association. While the speculative nature of this assessment was noted by Ehmann himself, it nevertheless exerted a bias on many of the attempts to locate the species. The grassland habitat in which we have found the species is difficult to search casually for reptiles, and consequently has received little attention. This is especially so because most grassy terrains in this part of South Australia are assumed to be heavily disturbed, supporting only the most wide-ranging and ecologically tolerant reptiles. The distinction between native versus introduced grasslands has been important in locating populations of this species.

Even when one knows the correct habitat, the shy nature of the lizards makes them very difficult to find unless it is known exactly how and where to search. The crucial piece of information that allowed us to locate additional colonies was the discovery of their dependence on spider holes, information that was only acquired after we had located the initial population through good luck. The holes are difficult to see unless the observer is right next to them, so that any lizard occupant has plenty of warning of human approach and is out of sight by the time the hole has been noticed. Intensive field work had been going on for six weeks at the site before we observed any *T. adelaidensis* under natural conditions. However, having discovered the combination of habitat and microhabitat, we have been able to locate further populations of pygmy bluebongues in nearby areas. The species is now known to occur at six sites running from south of Burra to north of Hallett, the extremes separated by about 50 km.

The apparent rarity, caused by lack of attention to grasslands as a habitat, is probably coupled to a drastic reduction in abundance caused by pasture improvement and cropping. Native grassland similar to that in which the species occurs at Burra once extended south on to the Adelaide plains, but as prime agricultural land, was one of the first major habitats in South Australia to be cleared and ploughed. Ploughing permanently alters the vegetation and ground cover, converting a native, largely perennial flora into an introduced, largely annual one. In addition, ploughing would destroy the burrows, killing lizards directly and leaving the survivors without shelter and at the mercy of predators. The fact that most specimens were collected last century may simply be correlated with the fact that this was when most of their habitat was being converted to agriculture.

Remaining native grassland is now extremely patchy, and the remnants have generally been heavily invaded by introduced annuals. However, populations of pygmy bluetongues have now been found in some of these remaining pockets, and provided that land use is not changed, these colonies may be relatively secure. Further work is focussing on finding the extent of the current range of the pygmy bluetongue, approximating population size within these areas, and confirming many of the subjective ideas developed during the course of this first season's field work. This will lead to an accurate assessment of the status of the species.

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Appendix I

Plant diversity at *Tiliqua adelaidensis* study site. Species noted during the general search but not recorded during step-pointing are indicated by (*). Taxonomy modified from Jessop (1989).

Species	Common Name	Annual/ Perennial	% Ground Cover
Native species			
Chenopodiaceae			
<i>Atriplex semibaccata</i>	berry saltbush	P	*
<i>Enchylaena tomentosa</i>	ruby saltbush	P	*
<i>Maireana aphylla</i>	cotton-bush	P	*
<i>M. enchylaenoides</i>	wingless bluebush	P	*
<i>M. trichoptera</i>	mallee bluebush	P	*
<i>Salsola kali</i>	roly-poly	A	*
Amaranthaceae			
<i>Ptilotus spathulatus</i>	pussytail	P	<1
Oxalidaceae			
<i>Oxalis perennans</i>	native sorrel	P	<1
Geraniaceae			
<i>Erodium cicutarium</i>	blue storks bill	P	*
Euphorbiaceae			
<i>Euphorbia drummondii</i>	caustic weed	P	*
Rhamnaceae			
<i>Cryptandra amara</i>	long-flower cryptandra	P	*
Thymelaeaceae			
<i>Pimelea micrantha</i>	silky riceflower	P	*
Rubiaceae			
<i>Asperula conferta</i>	common woodruff	P	*
Convolvulaceae			
<i>Convolvulus erubescens</i>	Australian bindweed	P	<1
Campanulaceae			
<i>Wahlenbergia luteola</i>	bluebell	P	*
Goodeniaceae			
<i>Goodenia pinnatifida</i>	cut-leaf goodenia	P	*
Asteraceae			
<i>Leptorhynchus squamatus</i>	scaly buttons	P	*
<i>Minuria leptophylla</i>	minnie daisy	P	*
<i>Vittadinia cuneata</i>	New Holland daisy	P	*
<i>V. gracilis</i>	woolly New Holland daisy	P	2
Liliaceae			
<i>Lomandra effusa</i>	scented mat-rush	P	1
<i>L. multiflora</i>	stiff mat-rush	P	4
Juncaceae			
<i>Juncus bufonius</i>	load rush	P	<1
<i>J. kraussii</i>	sea rush	P	<1
Poaceae			
<i>Aristida behriana</i>	brush wire-grass	P	*
<i>Danthonia caespitosa</i>	white-top	P	1
<i>D. pilosa</i>	velvet wallaby grass	P	3
<i>D. racemosa</i>	wallaby grass	P	<1
<i>Stipa blackii</i>	crested spear grass	P	<1
<i>S. eremophila</i> (possibly <i>S. puberula</i>)	desert spear grass	P	8
<i>S. nodosa</i>	spear grass	P	3
<i>Themeda triandra</i>	kangaroo grass	P	<1
Introduced			
Polygonaceae			
<i>Rumex dumosus</i>	wiry dock	P	*
Fabaceae			
<i>Medicago littoralis</i>	strand medic	A	6
<i>M. minima</i>	woolly burr medic	A	3
<i>Trifolium angustifolium</i>	narrow-leaf clover	A	3
<i>T. arvense</i>	hares foot clover	A	2
Boraginaceae			
<i>Echium plantagineum</i>	salvation Jane	A	8
<i>Neotostema apulum</i>	hairy sheepweed	A	7
Lamiaceae			
<i>Marrubium vulgare</i>	horehound	A	*
<i>Salvia verbenaca</i>	wild sage	P	14
Asteraceae			
<i>Arctotheca calendula</i>	Cape weed	A	*
<i>Carthamus lanatus</i>	saffron thistle	A	*
<i>Hypochoeris glabra</i>	smooth catsear	A	<1
<i>Sonchus oleraceus</i>	common sow-thistle	A	*
Iridaceae			
<i>Gynandriris setifolia</i>	thread iris	A	<1
Poaceae			
<i>Avena barbata</i>	bearded oat	A	23
<i>Brachypodium distachyon</i>	false brome	A	*
<i>Bromus rubens</i>	red brome	A	1
<i>Hordeum glaucum</i>	northern barley grass	A	*
<i>Lolium perenne</i>	perennial ryegrass	A	<1
<i>Vulpia murilis</i>	rats-tail fescue	A	2

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Summary

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Moorowipora chamberensis gen. et. sp. nov., an Early Cambrian coral with a morphology close to tabulates, occurs in the Moorowie Formation of the eastern Flinders Ranges. The oldest accepted tabulate coral *Lichenaria* Winchell & Schuchert first appeared in the Early Ordovician. However, it is possible that *Moorowipora chamberensis* is an early representative of the tabulates, extending their time range down to the Lower Cambrian. The tabulate-like characteristics of *Moorowipora chamberensis* include the form of the corallum, which varies between cerioid and fasciculate, the wedge-shaped to spine-like septa and generally complete, well-formed, convex-upward or undulating horizontal tabulae. *Moorowipora chamberensis* has some skeletal structures in common with the Early Cambrian species *Flindersipora bowmani* Lafuste, and *Tabulaconus kordae* Handfield, but is unlike other previously described Cambrian coralomorph.

Key Words: *Moorowipora chamberensis*, Early Cambrian, Moorowie Formation, tabulate coral, Flinders Ranges, South Australia.

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Introduction

The Early Cambrian coral *Moorowipora chamberensis* gen. et sp. nov., is found in slumped reefal blocks within a megabreccia forming part of the Moorowie Formation in the eastern Flinders Ranges of South Australia. *Moorowipora chamberensis* occurs with *Flindersipora bowmani* Lafuste 1991, and at least three other previously underscribed corals at a site close to the disused Moorowie Mine (Fig. 1).

Most of the several known Cambrian coralomorphs have been regarded as doubtful early representatives of tabulate corals. They show unusual aspects in their morphology; a significant gap in time (~20 my) occurs between the Early Cambrian and the oldest accepted Early Ordovician tabulate coral, *Lichenaria* Winchell & Schuchert 1895 (Scrutton 1979; 1984; 1992). *Moorowipora chamberensis* has structural characteristics suggesting its affinity with the tabulates, and is possibly an early representative of this group.

Stratigraphy and associations

The Moorowie Formation and its lateral equivalents, the Wilkawillina Limestone, Mernmerna Formation [= Parara Limestone, Dalgarno & Johnson (1962)] and Oraparinna Shale, form part of the Early Cambrian Hawker Group (Dalgarno 1964). These units are mainly limestones, calcareous shales and mudstones,

and siltstones, with minimal siliciclastic arenites, and variously reflect shallow marine, reefal, shelf-margin, slope and basinal environments of deposition.

The corals occur within reefal boundstones that have tumbled as large talus blocks to form a megabreccia, which comprises the middle part of the Moorowie Formation (Mount 1970¹; Hart 1989²; Lafuste *et al.* 1991; Savarese *et al.* 1993). This stratigraphic level represents part of a suggested third transgressive/highstand phase of the Early Cambrian (Gravestock & Hibbert 1991).

The talus blocks of the Moorowie Formation, analagous to those in contemporaneous reefs, comprise Type 5 shelf margin build-ups (James & Gravestock 1990). The reefal system was established in a high energy marine environment encroaching on a marginal fan (Savarese *et al.* 1993). The fan comprises coarse breccia and is suggested to have formed as a result of local diapiric activity. However, we have not observed any reef structures in their original placement.

Coral colonies, together with archaeocyaths and the calcimicrobes *Renalcis* Vologdin 1932, *Girvanella* Nicholson & Etheridge 1878 and *Epiphyton* Borneman 1886 occur in transported reefal blocks, which vary from cobble size to about 10 m in maximum dimension. Within individual blocks, the organisms are commonly preserved in life position. The dominant faunal elements vary markedly between blocks, from archaeocyaths, to stromatolites and more rarely corals. These differences probably reflect mass collapse of different parts of a zoned reef complex of reasonably wide areal extent (the distinctive biofacies represented surely formed in areas some hundreds of metres broad implying that the main reef front had a fringing geometry). The rapid slumping of the talus into deeper water (presumably the fore-reef) probably protected the carbonate frameworks from vadose

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¹ MOUNT, T. J. (1970) Geology of the Mount Chambers Gorge region. B.Sc. Hons. thesis The University of Adelaide (unpubl.).

² HART, J. (1989) Lower Cambrian corals from Archaeocyathan-Epiphyton clasts within the Moorowie Formation megabreccia, northern Flinders Ranges, South Australia. B.Sc. Hons thesis, The University of Adelaide (unpubl.).

diagenesis, resulting in the remarkably pristine preservation of the fauna. The corals commonly form encrusting to upright, tall colonies, the latter up to 60–70 cm high. Individual colonies tend to be widely spaced.

Flinndersipora howmani has been found in bioherms in the lower Orparinna Shale at Ten Mile Creek (Fig. 1), as well as near the Moorowie Mine (Lafuste *et al.* 1991). At Ten Mile Creek, trilobite and echinoderm fragments form hash beds in the Orparinna Shale, and associated archaeocyaths have been correlated with Faunal Assemblage 9 (Daily 1956), which equates with the *Pararana juncea* Zone of Jell (1990; Lafuste *et al.* 1991). This stratigraphic correlation indicates that the Moorowie Formation is Botomian in age.

Preservation

Although complete recrystallization of the colonies has occurred, an indication of the primary micro-

structure of the skeleton can be seen in some patchy domains. Edges of the possible primary biocrystal platelets are distinguished by crenate to wavy lines of minute inclusions within the much coarser crystals comprising the recrystallised fabric. Narrow, lath-like zones showing irregular extinction under polarised light occur at some places approximately transverse to skeletal elements where secondary carbonate crystals penetrate the coral skeleton. This suggests a residual overprint of the original mineralogy disturbing the optical continuity of the subsequent recrystallisation. Apart from recrystallised spar, cavities surrounding corallites and within the calices may be filled with very fine sand or silt. It appears that during life, part or whole colonies may have been temporarily covered with a thin layer of sediment causing the death of some zooids. The survivors rejuvenated new parts of the corallum. Some colonies seem to have been eroded by rapid, energetic influxes of coarse sand (also noted on calcimicrobe encrustations and archaeocyaths), allowing only a few corallites to continue their growth. Fractures post-date growth and are often filled with very fine sediment (Figs 2 and 3C).

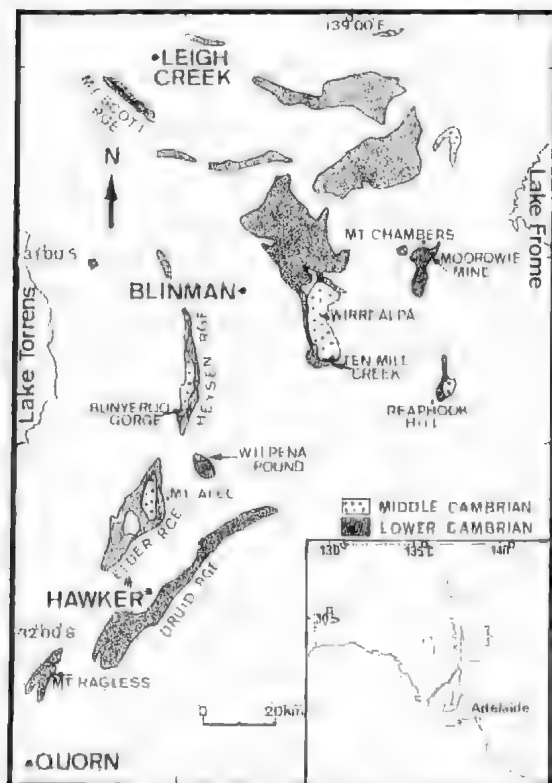


Fig. 1. Location map showing fossil occurrence near the Moorowie Mine and the distribution of Early and Middle Cambrian outcrops in the Flinders Ranges of South Australia.

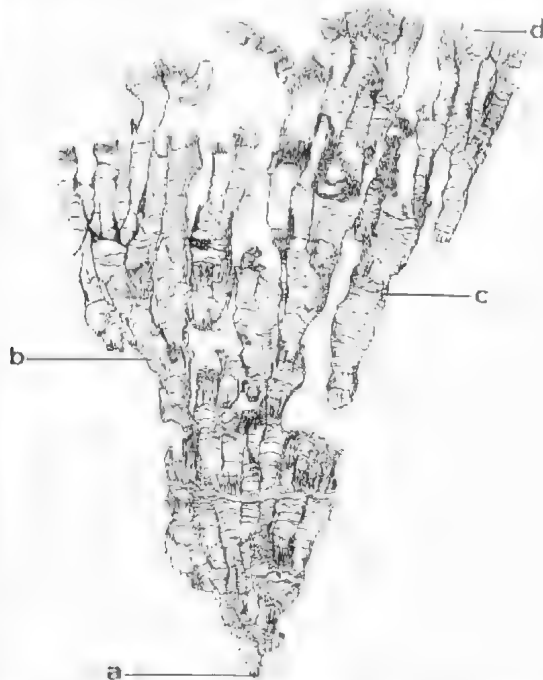
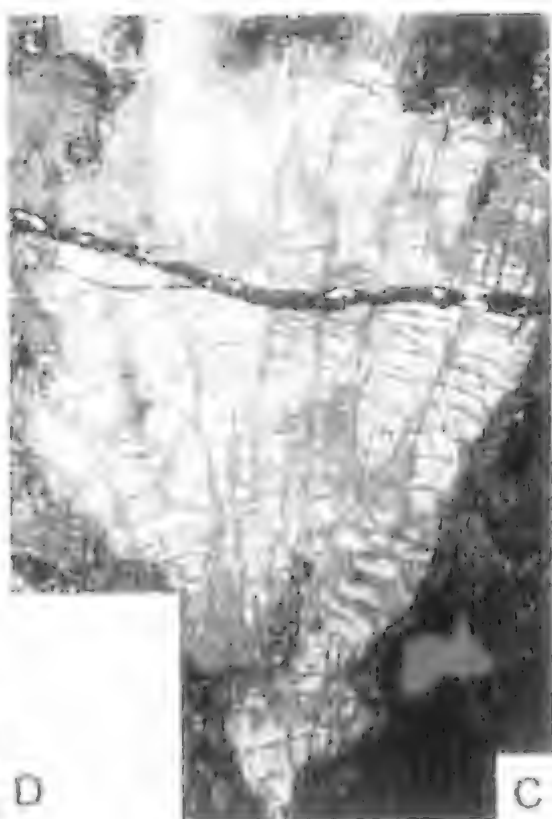


Fig. 2. Interpretive sketch (longitudinal section) of holotype SAM P34165, illustrating cone to fan shaped colony; the form of individual corallites; tabulae (b); septa (c); calice (d); lateral increase (top centre and right) and peripheral intra-calcular increase (x 2).

Fig. 3. Longitudinal sections of holotype SAM P34165, illustrating parts of the colony (see Fig. 2). A & B – Top of the colony with walls extending above the corallum, methods of increase and corallite structure: C – base of colony (x 1), and D – Higher magnification of (B) showing normal and thickened tabulae (lower left); and oblique projections of the outer wall (centre, right) (x 15).



D

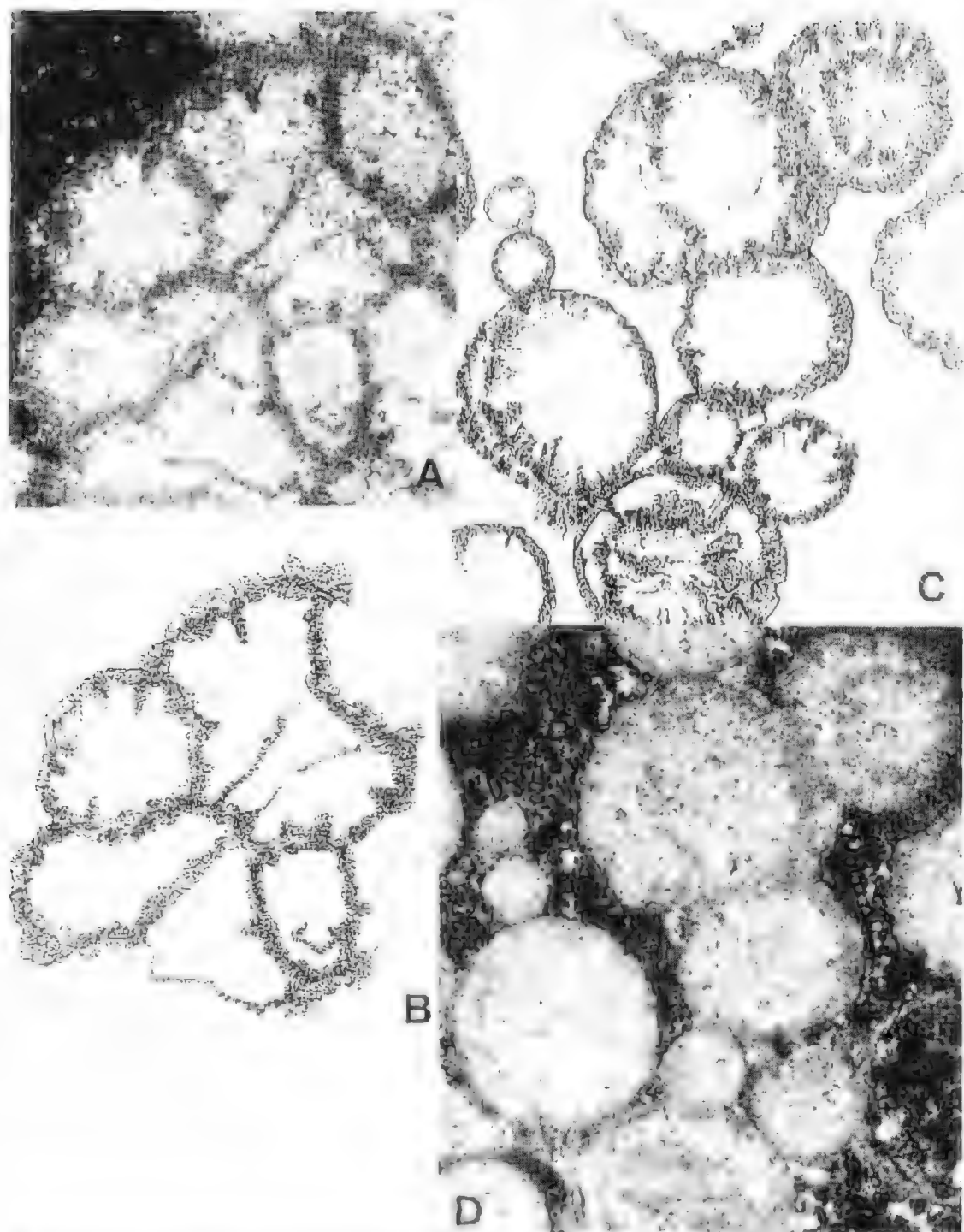


Fig. 4. Transverse sections and interpretive sketches of holotype SAM P34165: (A & B) cerioid ($\times 10$) and (C & D) fasciculate ($\times 10.5$) areas of the corallum. Differences can be seen in corallite shape, septa, and new walls across corallites formed during offset formation. Rejuvenation of corallites (C & D) is evident top right and bottom centre.

The term 'platelet' (Lafuste *et al.* 1991), is used to describe relic microstructural elements of the skeleton.

Systematic palaeontology

Phylum: CNIDARIA

Class: ANTHOZOA

Subclass: ?TABULATA

Family: uncertain

Genus: *Moorowipora* gen. nov.

Type species: *Moorowipora chamberensis* sp. nov.

Etymology: For the type locality near the Moorowie Mine in the eastern Flinders Ranges of South Australia.

Diagnosis: Corallum small, varying from massive cerioid to fasciculate, comprising polygonal, oval or rounded corallites. Corallites are long, tuberoid to irregularly cylindrical. Walls are thin, wavy to crenate, rarely straight. Tabulae are irregularly spaced, mostly complete, concave upwards to undulating horizontal. Septa absent, or number up to 20 in each corallite. Where present, septa are randomly spaced, short and form wedge to spine-like projections into corallites, arising from inward angulations of the wall. Pores appear to be absent.

Moorowipora chamberensis sp. nov.

FIGS 2-7

Etymology: For nearby Mt. Chambers.

Diagnosis: As for genus.

Type specimens: The specimens described in this paper are held at the South Australian Museum (SAM).

Holotype SAM P34165, four thin sections, SAM P34165-1; SAM P34165-2; **Paratypes** SAM 34166-1; SAM P34166-2.

Material: The holotype, paratypes as well as several other colonies come from one rock sample measuring 270 mm long, 230 mm wide and 120 mm thick: taken from a large boulder within the Moorowie Formation, near the Moorowie Mine in the eastern Flinders Ranges.

Description: In transverse section (Figs 4, 5), corallites show gradation into two distinct habits, massive cerioid and fasciculate dendroid. In fasciculate habit, corallites rarely touch, are circular to slightly oval in shape and vary in diameter from 0.95 to 3.75 mm. Corallites with massive habit are rather irregularly shaped 5 or 6 sided polygons, sometimes oval or rectangular, rarely circular; they vary individually in diameter from 0.77 to 3.5 mm.

Walls are thin, varying between 0.1 mm and 0.15 mm in thickness and show a relic fibrous structure (Figs 4-6).

A midline is apparent between many adjoining corallites. Walls are wavy to slightly crenate, being rounded in isolation or adjacent to small spaces in the corallum, with a tendency to become straighter and less distinct where they merge with the walls of adjoining corallites.

In longitudinal section (Figs 2, 3), each colony is generally small, numbering from 2 or 3 to about 16 corallites. Colonies are either cone- to fan-shaped, diverging outward from a single protocorallite, or more rectangular, where they appear to arise from several adjacent corallites. Increase is both lateral and peripheral intracalicular, producing 1, 2 or more offsets (Figs 2, 3A).

Individual corallites are tuberoid to irregularly cylindrical in shape and vary greatly in width and length (up to 19.5 mm), prior to increase (formation of a new corallite). The base is rounded and blunt, the protocorallite producing 3 or 4 short septa prior to the formation of an initial tabula. The calice is prominent extending between 2.5 and 4.75 mm past the last tabula (Figs 3B, 3D).

Tabulae are mostly complete, mainly convex-upward or undulating horizontal, often down-turned where they meet the wall (Figs 2, 3). They are irregularly spaced, but commonly occur at the same level in adjacent corallites. The distance between them is highly variable (0.35 to 2.1 mm), while the thickness of tabulae varies from 0.002 mm to 0.01 mm.

Septa number up to 20 in fasciculate corallites; are very short (0.01-0.2 mm), generally equal in length, triangular to wedge-shaped, often indistinct. They form protrusions of the wall of the corallite at sites of inward creasing (Figs 4, 5). In massive, cerioid corallites in the main body of the corallum, there may be up to 10 septa or septa may be absent. Septa are randomly spaced; long and short septa may alternate, or only long or short septa may be present. Septa are wedge to spine-like in shape. Septa are generally longer than in the fasciculate corallites. In longitudinal section septa are observed as continuous vertical laminar plates intersecting normally with tabulae.

Microstructure: The microstructure was studied at magnifications up to $\times 200$, and photographs were taken under polarised light.

In transverse section at low magnification (Figs 4, 5) relic fibrous elements which form the sclerenchyme and apparently represent indications of original bio-crystals appear as continuous lineae across the wall and into the septa. At higher magnification (Fig. 6) the interlocking fibrous elements form triangular to rectangular bundles, composed of narrow parallel-sided

and blade-like geniculate structures up to 164 μm long and 37 μm wide. These are angled towards and away from the centre of each corallum. The bundles have the appearance of crossing, or being stacked over underlying layers. Near the midline of walls the fibres are often less oblique and have a slightly different orientation, appearing to be broader and more randomly oriented.

In longitudinal section at magnifications of $\times 100$ to $\times 200$, the midplane of the wall seems to have been composed of irregularly shaped, crenate, interlocking platelets which individually represent the fibrous lineae of transverse cuts. Platelets may be almost rectangular, vertical to slightly inclined, occasionally almost horizontal in the middle of the wall. They commonly occur diverging outward towards the top of corallites (Fig. 7). Wall platelets are more elongate and wider than the fibre bundles seen in transverse section, being up to 190 μm in length and 138 μm in width.

Tabulae are continuous with the inner edge of the wall, which converges slightly around them. The structure of the tabulae is similar to the septa and wall

in transverse section, with bundles of fibres being mainly triangular, or irregularly shaped. Triangular bundles of fibres are up to 360 μm in length, and 308 μm in width. In tabulae of normal thickness, adjoining triangular bundles interlock forming a crenate

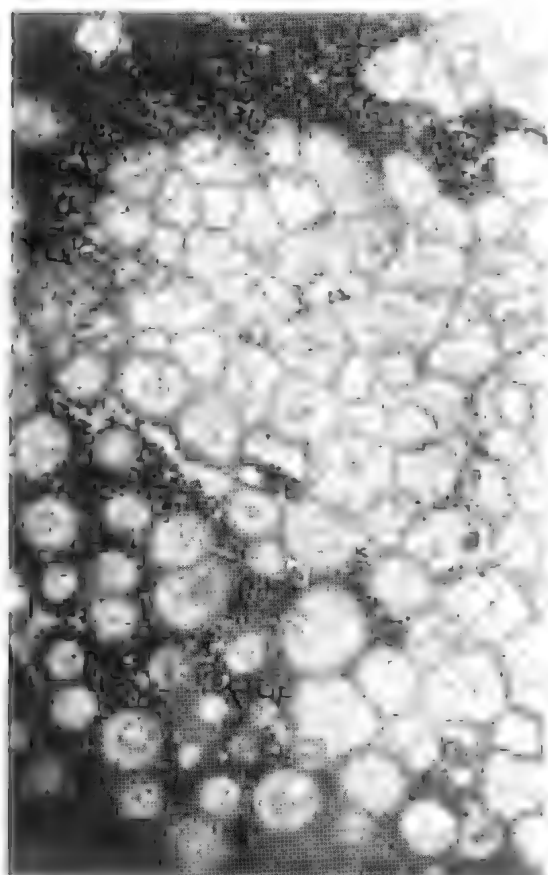


Fig. 5. Transverse section of holotype SAM P34165: part of corallum showing both corioid and fasciculate areas ($\times 3.3$).

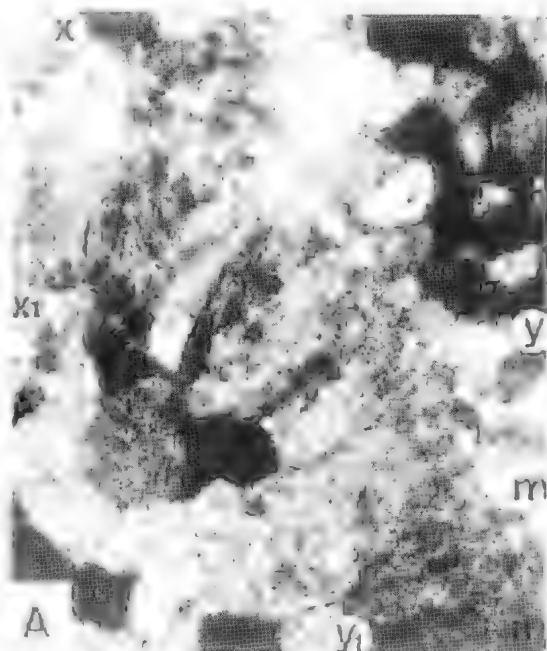


Fig. 6. Transverse section and interpretive sketch of holotype SAM P34165: illustrating triangular and rectangular bundles of fibres extending across the walls of the corallum. x-x1 and y-y1 define boundaries of illustration, m is midline of the wall ($\times 44$).

upper and lower surface. A more complicated interlocking pattern is formed in thickened tabulae.

Remarks: *Moorowipora chamberensis* is dimorphic in both the morphology of the colony and the method of increase. Dimorphism often occurs in tabulates and may be shown as differences in corallite size, shape and internal structures (Oliver 1968, 1975). Many intraspecific variations are probably environmentally controlled, being influenced by factors including the adjacent sediment, and the position of corallites within a colony (Oliver 1968). The two different morphological forms observed in *M. chamberensis* probably reflect the mode of increase, which also appears to be dimorphic, being related to the position of individual corallites within the corallum. Corallites within the fasciculate area, which generally occurs at the outer edges of the colony, appear to have resulted from lateral increase. Offsets branch away from the main colony producing isolated corallites which rarely touch and are therefore unaffected by crowding (Figs 2, 5). Such corallites are thus round to slightly oval

in transverse section. Peripheral intracalicular increase is most common in the massive, acrioid parts, and where a solitary corallite has become established (Figs 2, 3). Usually one, two or more offsets are produced at the same time, with new walls growing from sites of septal insertion across the calice. Both methods of increase commonly occur at different stages of growth within the same corallite, and are probably related to the amount of space surrounding it.

The variable distance between tabulae and the presence or absence of septa do not appear to be linked to any particular stage of growth, a characteristic which has been suggested as possibly occurring in some tabulates (Hill 1981). Septa primarily occur in the protocorallite and immature corallites, while at other stages of growth they may or may not be present.

Discussion and Conclusion

When compared with other Cambrian corals suggested to have tabulate affinities (Scrutton 1979), *Moorowipora chamberensis* is closest in its morphology to *Tabulacodus kordae* Handfield 1969, from the Early Cambrian (Botolphian) of east central Alaska and British Columbia. In vertical section, *M. chamberensis* and *T. kordae* differ in the shape of the corallites, which are more tubular in appearance in the former. Height and width vary, with mature corallites being up to 19.5 mm long and 5.0 mm wide in *M. chamberensis*, while corallites of *T. kordae* are up to 65 mm long and 27 mm in width in the colonial form (Debrenne *et al.* 1987). The tabulae also differ, being undulating horizontal to concave upward in *M. chamberensis* and either horizontal or slightly concave downward in *T. kordae*. Incomplete tabulae are more dissepiment-like and walls are generally thicker in the latter (Handfield 1969). The microstructure of both corals is significantly different in transverse section, being geniculate fibres in *M. chamberensis*, and concentric light and dark wavy laminations in *T. kordae*. Tabulae also differ, being formed from bundles of fibres extending upward and downward from a medial line in the former, unlike the two layered light and dark zones of *T. kordae*. However, platelets (longitudinal section) in the walls of *M. chamberensis* are of similar shape, but generally larger. *M. chamberensis* may belong in the family Tabulacodidae, but, the above differences, likely preclude it from this division.

M. chamberensis is distinguished from *Lipopora lissa* and *L. daseia* Jell & Jell 1976, from the Early Middle Cambrian of western New South Wales, by the presence of tabulae and the shape and arrangement of septa, although the corallites of *L. lissa* are of similar length and width. *Cambroirypa montanensis* Fritz & Howell 1955, from the Middle Cambrian of British

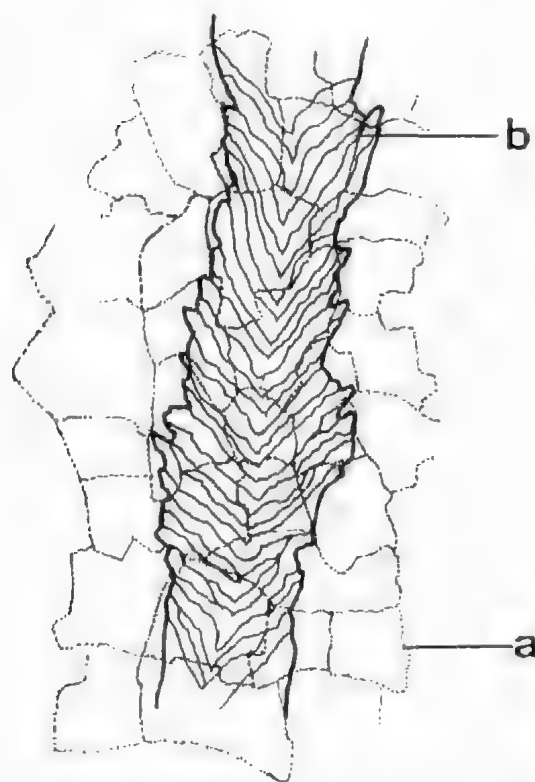


Fig. 7. Longitudinal section (cartoon sketch) showing large crystals of the recrystallisation fabric (a) incorporating the wall of compound corallites. (b) Relic biocrystal fibres diverge towards the corallum.

Columbina, is distinguished from *M. chamberensis* by the more slender corallites and the absence of tabulae and septa. Most of the Early Cambrian coraiomorphs described by Korde (1963, 1984a, b, 1986, 1990), are partly synonyms of already described khasaktiids or hydroconochoans and partly *nomen dubium* or *nulla* (Zhuravlev *et al.*, 1993, p. 369).

M. chamberensis also differs from *Flindersipora bowmani* Lafuste 1991, although there are some similarities in microstructure. *M. chamberensis* is cerioid to fasciculate and has wedge to spine-shaped septa up to 0.2 mm in length arising from continuous walls 0.1–0.15 mm thick. In contrast *F. bowmani* is meandroid to cerioid, and has 6–16 strongly developed, straight to slightly curved septa up to 0.8 mm in length, with the edges of septa bearing very short blunt spines. Walls form very short segments between the septa and are 0.15–0.25 mm in thickness (Lafuste *et al.*, 1991). In *F. bowmani* tabulae are mostly concave-downward, and closely spaced (0.2–0.3 mm), but are undulating horizontal to concave and more regularly spaced in *M. chamberensis*. The mode of increase is by longitudinal fission in the former while both lateral and intercalicular peripheral increase occurs in the latter.

In transverse section, the microstructure of both corals is similar, with walls consisting of geniculate fibres which diverge and converge in two directions. In vertical section platelets in *M. chamberensis* are less elongate and broader when compared with *F. bowmani*.

It is considered that the genus *Lichenaria* which has a time range from the basal to the early/late Ordovician is the most ancient tabulate coral. Its colonial form is cerioid, it has a simple morphology

and tabulae, is aseptate, and may have rare mural pores (Bassler 1950; Flower 1961; McLeod 1979; Scrutton 1984; Laub 1984). *M. chamberensis* has structural characteristics which demonstrate its affinity to the tabulates (including septa, which are not present in lichenariids). These are (1) the cerioid to fasciculate form of the colony; (2) the spine-like to wedge-shaped septa; (3) its mode of increase; (4) the generally complete well-formed tabulae. The observed relic microstructure appears to be similar to the pinnately (clinogonally) fibrous structure of some tabulates (see Hill 1981, p. F452), including lichenariids, though the extent of the modifying influence of diagenesis is uncertain.

M. chamberensis with its tabulate-like characteristics may be either an early representative of the tabulates, or belong to a new group of corals with convergent evolution contributing to their similarities. These alternatives have been suggested by Lafuste *et al.* (1991) for *F. bowmani*, whereas Scrutton (1992), regards the latter possibility as most likely. The addition of *M. chamberensis* to the group of known early coraiomorphs, provides further evidence that tabulate corals may have their origin in the Early Cambrian.

Acknowledgments

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**NOTES ON THE MORPHOLOGY AND BIOLOGY OF
CTENOPHORUS MCKENZIEI
(STORR, 1981) (SQUAMATA: AGAMIDAE)**

BY M. PETERSON^{}, G. M. SHEA[†], G. R. JOHNSTON[‡] & B. MILLER[§]*

Summary

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The systematic status of *Ctenophorus mckenziei* is reviewed, on the basis of additional material from Western Australia and South Australia. Habitat data for known localities, stomach contents, one record of clutch size, and behavioural observations and thermal preferences of captive individuals are provided. *C. mckenziei* is morphologically very similar to *C. scutulatus*, differing mainly in adult size and subtle modifications of colour pattern. *C. mckenziei* and *C. scutulatus* are phenetically most similar to *C. cristatus*.

Key Words: Squamata, Agamidae, *Ctenophorus*, morphology, biology, habitat, diet, thermal biology.

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KEY WORDS: Squamata, Agamidae, *Ctenophorus*, morphology, biology, habitat, diet, thermal biology.

Introduction

The agamid *Amphibolurus mckenziei* was described from two specimens (Western Australian Museum [WAM] R59753-54), collected at 5 km and 8 km SW of Ponier Rock, Western Australia (Storr 1981). The species was subsequently transferred, with a number of other agamid species, to *Ctenophorus* (Storr 1982). Additional specimens of *C. mckenziei* have since been reported from Western Australia and South Australia by Schwaner & Tyler (1985), McKenzie *et al.* (1987), Anon. (1988), Wilson & Knowles (1988), Armstrong (1992) and Ehmann (1992). This additional material, previously uncharacterised, considerably extends our knowledge of the morphology, distribution and habitat preferences for this species and provided the basis for this paper.

Materials and Methods

Five specimens from Western Australia, additional to the types, have been collected: South Australian Museum (SAM) R2832, Western Australia; WAM R91764-65, 9 km E Kilidwerinia Granite Rock, 32°04'S 124°00'E, 29.iii.1984; WAM R91842, R91852, 15 km E Kilidwerinia Granite Rock, 32°03'S 124°05'E, 5.x.1984. Eleven specimens have been collected from South Australia: SAM R25572, R26162, 12.6 km (air distance) NE 'Colona', 31°31'S 132°09'E; SAM R26160-61, 16.2 km (air distance) NE 'Colona', 31°31'S 132°11'E; SAM R26890, 15.2 km (road

distance) NE 'Colona', 31°31'S 132°09'E, 13.xi.1984; SAM R32264-65, R32268-69, 0.5 km S Mitcherie Rockhole, Yumburra Conservation Park, 31°27'S 132°49'E, 17.x.1987; SAM R32266-67, 5 km S Mitcherie Rockhole, Yumburra Conservation Park, 31°29'S 132°50'E, 18.x.1987 (Fig. 1).

Measurements taken on preserved material follow those used by Shea & Peterson (1985). Log-transformed morphometric data were statistically analysed with analysis of covariance, using the SYSTAT statistical package (Wilkinson 1987).

Dietary data were obtained by examining stomach contents of six specimens: SAM R2832, R25572, R26160-62, WAM R59753.

Four specimens were maintained alive for some time following collection. The lizards were housed in a vivarium with a heat lamp and fluorescent lighting, both turned on at 0630 h and off at 1930 h.



Fig. 1. Distribution of *C. mckenziei*.

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corresponding to the local natural photoperiod at that time. Water, mealworms and chopped fruit were available *ad libitum*. However, one individual (R32266) became emaciated and was euthanased. At 1800 h on 11.xii.1987 (i.e., 54–55 d post capture) the remaining three lizards were placed in a thermal gradient (8–60°C), and allowed to acclimate. Calibrated copper-Constantan thermocouples were placed at least 20 mm into the cloaca and held in position with surgical tape. Cloacal temperatures were electronically recorded every 10 min, for each animal from 1130 h on 12.xii.1987 to 1130 h on 13.xii.1987. Any temperatures taken while lizards were tangled in the thermocouples were excluded from the analysis.

Thermal data were analysed using a one-way ANOVA to test for differences in thermal preferences between individuals. In comparing thermal preferences during scotophase and photophase, data from all individuals were pooled.

Results

Morphology

The South Australian sample (snout-vent length [SVL] 41.76 mm, \bar{x} = 63.5 mm, n = 11) is similar in morphology and colouration to the Western Australian sample (SVL 31.5–71.5 mm, \bar{x} = 58.4 mm, n = 7). There are minor, but statistically significant differences between the two (Table 1) in the relationship between tail length (TL) and snout-vent length (slopes: $F_{1,13}$ = 5.477, p < 0.05; overall, TL/SVL 215.0–252.9%, \bar{x} = 233.5%, n = 11 vs 206.3–236.9%, \bar{x} = 222.5%, n = 6 respectively) and between head depth (HD) and head length (HL) (slopes: $F_{1,13}$ = 9.900, p < 0.01; overall, HD/HL 57.7–67.9%, \bar{x} = 61.4%, n = 11 vs 62.0–67.5%, \bar{x} = 64.0%, n = 7 respectively), with the eastern juveniles having a longer tail and the eastern adults a more depressed head. It is possible that the apparent long tail on eastern juveniles may be an artefact due to the lack of very small juveniles in the sample.

The affinities of *C. mckenziei* have not previously been adequately defined. Storr (1981) assumed a close affinity with *C. scutellatus* (Stirling & Zeitz, 1893), but provided no argument for this. The *C. mckenziei* material now at hand clearly indicates that this species is very close to *C. scutellatus*. Head, body and limb proportions are similar, the arrangement of spine clusters, rows of enlarged scales and skin folds on the head, neck and body is identical, and most elements of the colour pattern are shared. Both species have the following colouration elements (Fig. 2):

1. a pale vertebral stripe, bordered by
2. a dark paravertebral stripe, bordered laterally by

3. a longitudinal series of pale blotches, coalescing anteriorly and often posteriorly to form an irregular stripe from behind eye, over the ear and upper postauricular spines, to the tail base, where the two stripes often fuse. This element is bordered laterally by
4. an upper lateral zone from below the eye, through the ear, over the forelimb and hindlimb to the proximal part of the tail, bordered ventrally by
5. a broad pale midlateral stripe from axilla to groin, then along hind edge of thigh along the proximal part of the tail, dark margined ventrally;
6. on nape and forebody, a series of dark transverse bars connecting the dark paravertebral stripes and interrupting the pale vertebral stripes;
7. narrow pale caudal rings usually present, overlying other elements of tail pattern;
8. dark ventral markings in males and some females consisting of at least a broad median stripe from chin to gular fold, broadest just rostral to the gular fold, and a rhomboidal to kite-shaped dark breast patch, extending caudally a variable distance, in some cases to the groin. Some specimens of both species have additional dark ventral markings, including streaks and spots laterally on the throat, and dark anterior margins to the thighs (Fig. 3).

Storr (1981) differentiated *C. mckenziei* from *C. scutellatus* by four characters: smaller size, deeper head, fewer subdigital lamellae on the fourth toe and colouration (back blackish brown with whitish vertebral stripe and transverse lines vs pale brown with paired dark brown blotches merging on foreback to form crossbands). The additional material now available supports the size difference (SVL = 31.5–76.5 mm vs 31–115 mm; Storr *et al.* 1983). The smallest male *C. mckenziei* with dilated, wax-filled femoral and preanal pores and turgid testes has SVL = 48 mm (SAM R25572), while a female of the same size (SAM R26890) has well-developed ovaries and oviducts. One female (SAM R2832, SVL = 71.5 mm) is gravid, with three oviducal eggs. However, the remaining three characters employed are non-diagnostic or require qualification.

The purportedly deeper head of *C. mckenziei* is not apparent in our measurements (Table 1), although it is clear from the very much lower values given by Storr (1981) that he used different measurements to obtain a head depth/head length ratio (possibly head depth as defined by Witten [1985]). We have measured head depth at the highest point of the skull, over the parietal eye, and head length from tip of snout to rostral margin of ear. As noted above, the eastern sample of adult *C. mckenziei* had a shallower head than the western sample. A difference of similar magnitude was also present between the eastern sample and *C. scutellatus* (slopes: $F_{1,28}$ = 8.814, p < 0.01).

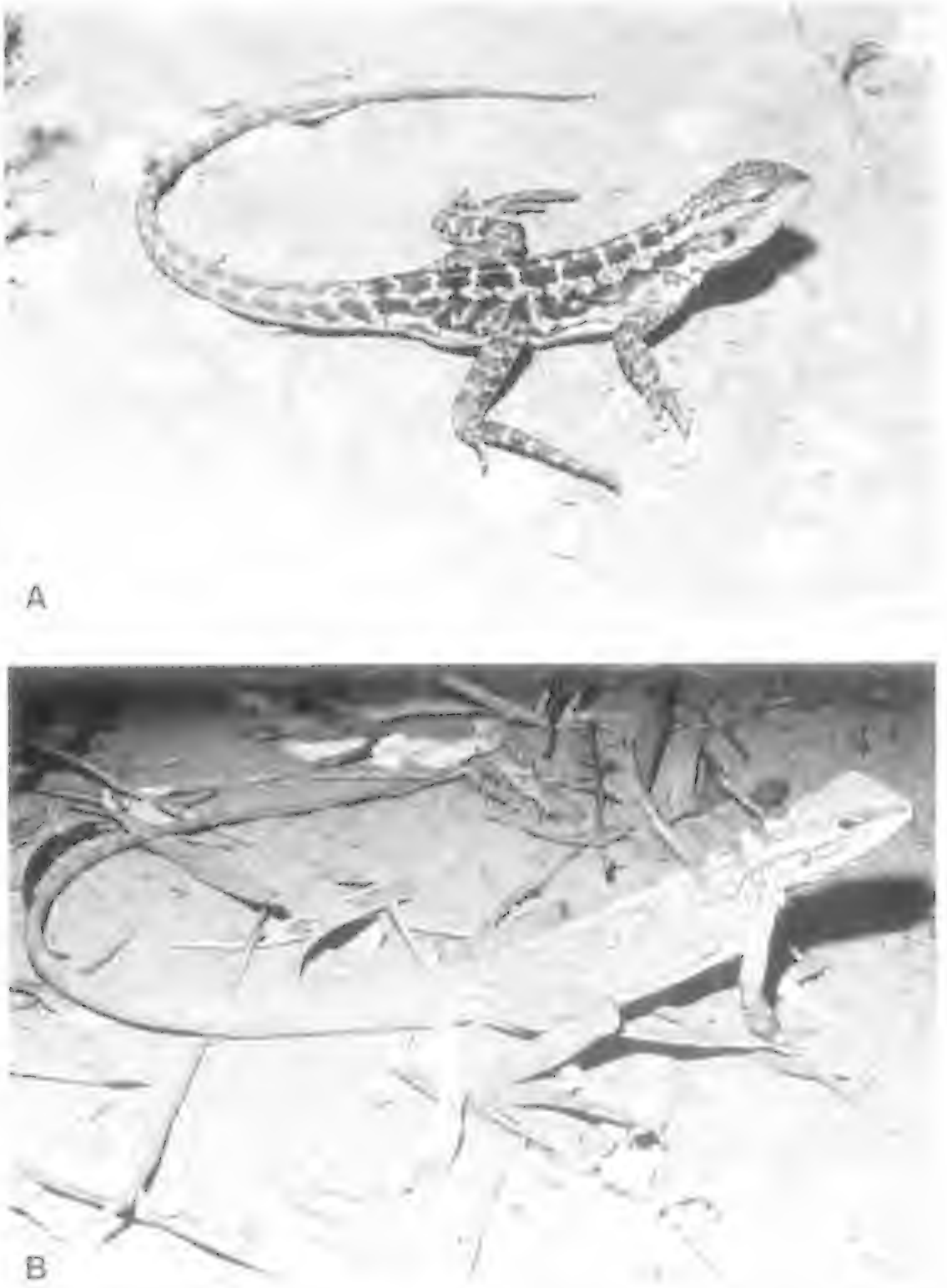


Fig. 2. Dorsolateral views of A. male *C. mckenziei* (15.2 km NE "Colona", SA) and B. male *C. scutulatus* (Hospital Rocks, WA) in life (photographs M. Peterson).

The lower number of subdigital lamellae in *C. mckenziei* is not an absolute difference, and is geographically variable. Western *C. mckenziei* had counts of 25–30 (\bar{x} = 27.4, mode = 27, n = 14) while eastern *C. mckenziei* had 25–32 (\bar{x} = 29.6, mode = 30, n = 18). The *C. scutellatus* sample we examined had 28–41 (\bar{x} = 34.9, n = 80) subdigital lamellae, only 7.5% fewer than 32, although Storr *et al.* (1983) give a range of 31–44. All means are significantly different (pairwise *t*-tests: eastern vs. western *C. mckenziei*, t_{30} = 3.36, p < 0.05; western *C. mckenziei* vs. *C. scutellatus*, t_{92} = 10.88, p < 0.005; eastern *C. mckenziei* vs. *C. scutellatus*, t_{96} = 8.33, p < 0.005).

As noted above, the colour pattern is composed of the same elements in each species. The difference noted by Storr (1981) is due to paling of the dark dorsal markings in *C. scutellatus*, particularly the centres of such markings, and enlargement of the pale dorsal spots. The dark crossbands on the foreback of *C. scutellatus* are also present in *C. mckenziei*, though narrower, less contrasting and often fewer.

Sympatry is not yet known between *C. mckenziei* and *C. scutellatus* to confirm a species-level difference,

although the two species are known to approach to within 85 km of each other (WAM R91764–65 vs R65538, 0.5 km S Buninongia Spring, respectively). However, the lower number of subdigital lamellae in western *C. mckenziei*, which are geographically closest to *C. scutellatus*, together with the much smaller adult size, and consistent evenly dark upper lateral zone (vs. usually light centred) suggest that *C. mckenziei* is specifically distinct.

Habitat

The two Western Australian localities listed above, and the two South Australian localities 12.6 km NE and 16.2 km NE "Colona" are respectively sites BA2B, BA5, KO2 and KO4 of McKenzie & Robinson (1987), while the localities 0.5 km S and 5 km S Mitcherie Rockhole are sites MI51 and MI21 of Copley & Kemper (1992). From the combination of photographs of the habitat and floristic lists at each locality provided by McKenzie & Robinson (1987) and Copley & Kemper (1992), specimen collection data from both museums and observations by the senior author, it appears that the primary floristic components of the *C. mckenziei*

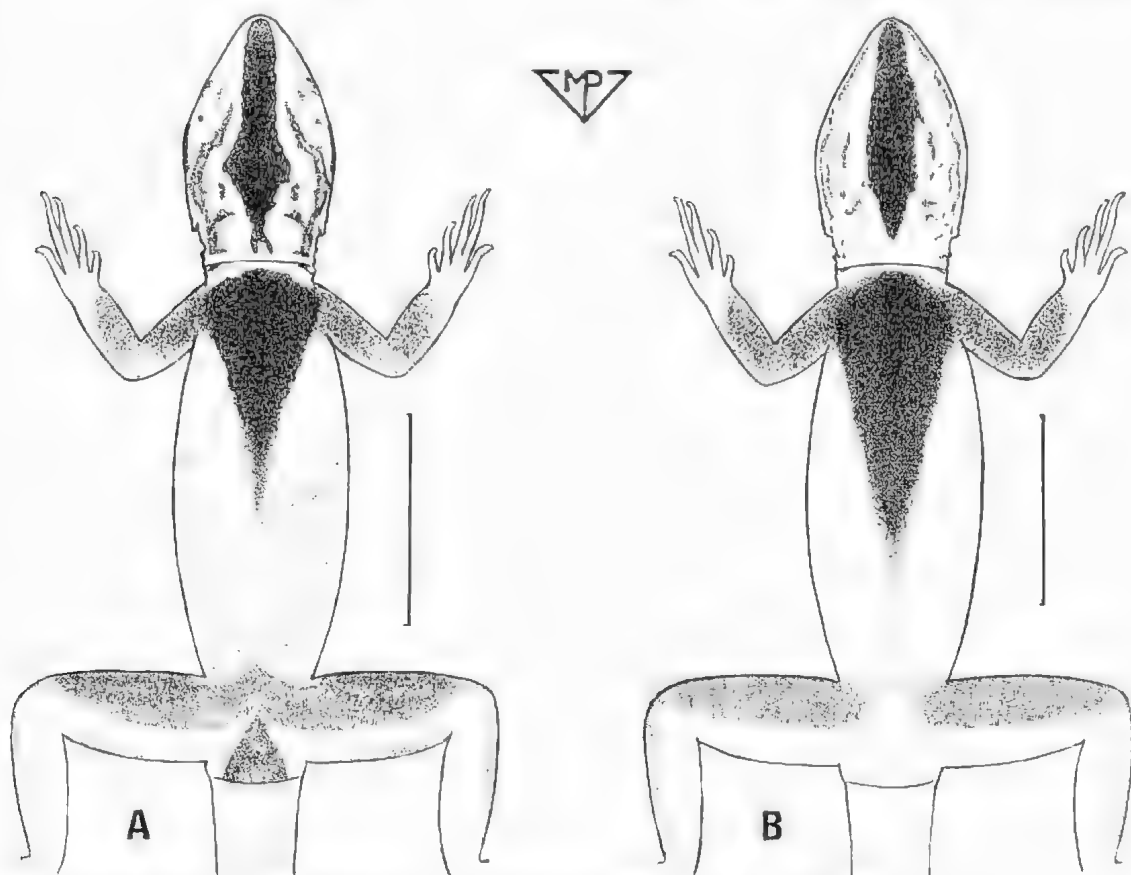


Fig. 3. Typical melanin ventral patterns of A. *C. mckenziei* and B. *C. scutellatus*. Scale bars = 2 cm

habitats are *Eucalyptus oleosa* Ev.M. ex Miq. (giant mallee), *Acacia oswaldii* Ev.M. (umbrella wattle) and *A. papyrocarpa* Benth. (western myall) over a chenopod understorey of *Atriplex vesicaria* Howard ex Benth. (saltbush), *Maireana* spp. (bluebush), *Rhagodia spinescens* R.Br. and *Sclerolaena* spp. The chenopod understorey is common to all localities. The substrate type at sites BA2B, BA5, KO2, KO4 and MI5I is crusting sandy clay loam to loam (McKenzie & Robinson 1987; Copley & Kemper 1992), while the specimen from 15.2 km NE "Colona" was found under a bluebush on a non-crusting sandy substrate, similar to the substrate recorded from site MI2I.

At sites BA2B, BA5, KO2, KO4 and 15.2 km NE "Colona", *C. mckenziei* was sympatric with *C. pictus* (Peters 1866), and at the former three sites it was also sympatric with the agamid *Tympanocryptis lineata* Peters 1864. At site MI2I, it was the only agamid recorded, while at site MI5I, *C. fordii* (Storr 1965) and

Pogona minor (Sternfeld 1919) were also recorded. The latter species was also found at 15.2 km NE "Colona".

Diet

The dominant prey items in all specimens examined were ants, particularly small *Iridomyrmex*, although some larger ants (*Camponotus*, *Melophorus* and other unidentified genera) were present. Other prey items recorded were Hemiptera (single individuals of *Poecilometis* sp. in R22835, R2832, two pentatomids in R2832, and a small unidentified bug in R26162), Coleoptera (one small curculionid prothorax and a large scarab larva in R2832; three unidentified elytra in R25572), Mecoptera (a large abdomen in R2832), Diptera (one small fly wing in R2832), Homoptera (one small wing in R25572), Orthoptera (one small grasshopper head in R25572), Hymenoptera (one small bee head in R25572) and flower parts (R26161).

TABLE 1. Allometric equations and calculated values for cranial and somatic proportions in *C. mckenziei* (mek), *C. scutellatus* (scu) and *C. cristatus* (cri). Eastern and western samples of *C. mckenziei* are kept separate for tail length and head depth, but pooled elsewhere, as the equations were not significantly different. Values *a* and *b* solve the equation $y = bx^a$, s.e. is standard error of *a*, r^2 = correlation coefficient, al. = direction of significant allometry, C_{32} , C_{76} and C_{105} are calculated percentage proportions at SVL = 32, 76 and 105 mm (approximate minimum size for all species, maximum size of *C. mckenziei* and approximate large adult size for both *C. scutellatus* and *C. cristatus*).

	a	s.e.	b	r^2	al.	C_{32}	C_{76}	C_{105}
	AGL/SVL							
mek	1.2128	.0535	.183	.9698	+	.37	.46	—
scu	1.0699	.0284	.323	.9868	+	.41	.44	.45
cri	1.0847	.0381	.295	.9854	+	.40	.43	.44
	TL/SVL							
mek(E)	.9732	.0648	2.606	.9617	0	2.37	2.32	—
mek(W)	1.1662	.0423	1.145	.9948	+	2.04	2.35	—
scu	1.1020	.0348	1.586	.9843	+	2.26	2.47	2.55
cri	1.1582	.0282	1.104	.9930	+	1.91	2.19	2.31
	FLL/SVL							
mek	.8350	.0382	.785	.9677	—	.44	.38	—
scu	.9254	.0348	.573	.9739	—	.44	.41	.40
cri	.9706	.0300	.476	.9887	0	.43	.42	.42
	HLL/SVL							
mek	.8714	.0339	1.503	.9763	—	.96	.86	—
scu	.9166	.0311	1.275	.9797	—	.95	.89	.86
cri	.9911	.0196	1.017	.9953	0	.99	.98	.98
	HL/SVL							
mek	.7939	.0458	.530	.9493	—	.26	.22	—
scu	.8563	.0223	.421	.9873	—	.26	.23	.22
cri	.7613	.0179	.631	.9934	—	.28	.22	.21
	HW/HL							
mek	.8719	.0231	1.234	.9889	—	.94	.86	—
scu	.8950	.0175	1.206	.9928	—	.97	.89	.87
cri	.8995	.0193	1.217	.9945	—	.98	.92	.89
	HD/HL							
mek(E)	.7185	.0671	1.286	.9272	—	.71	.58	—
mek(W)	.9809	.0473	.673	.9885	0	.65	.64	—
scu	.9312	.0280	.756	.9831	—	.65	.62	.61
cri	.9669	.0287	.726	.9896	0	.68	.66	.66

Behaviour

Two types of circumduction and two types of head-bob were seen. The circumduction types seem to correspond to the challenge wave and submissive wave described by Brattstrom (1971) in *Pogona barbata* (Cuvier 1829). The head-bobs differed in cadence and degree to which the head was moved, aided by extension of the forelimbs. In a dominant male the head was moved a greater distance below and above the normal plane at a faster rate than it was in a subordinate male or two females.

Two captive males were observed in an agonistic display. Upon being placed in the enclosure for acclimation, they head-bobbed and circumducted several times before presenting to each other at a distance of about 15 cm. They were facing in the same direction and continued to head-bob. As the display intensified they coiled their tails loosely and both did several hind-leg push-ups, similar to those described for the *C. decreesii* complex by Gibbons (1979). The display ended when one lizard bit the other on the nape. They rolled violently about the cage and then separated.

Temperature preferences

The three *C. mckenziei* studied maintained body temperatures between 11.1°C and 43.4°C ($\bar{x} = 34.7^\circ\text{C}$, $\sigma^2 = 3.41$) in a thermal gradient over a 24 h period (Table 2). There were significant differences in thermal preferences between individual lizards ($p = 0.04$). This may have been due to the low variance of R32267 with respect to the other two individuals. Differences between nighttime and daytime body temperatures were barely significantly different ($p = 0.05$). However there was a large difference in voluntary minimum body temperature during photophase (11.1°C) and scotophase (28.7°C). This may reflect greater

activity during the day. Interestingly, the voluntary maximum body temperature (43.4°C) was achieved during the night, indicating that some nocturnal activity occurred.

Discussion

Morphology and relationships

The affinities of *C. mckenziei* and *C. scutellatus* to other taxa remain uncertain. Pianka (1971) stated, without providing evidence, that *C. scutellatus* and *C. cristatus* (Gray 1841) were 'obviously rather closely related'. Moody (1980)¹ added the *C. caudimaculatus* group to the latter complex, diagnosing it on the basis of shape of the medial process of the prearticular bone, limb length, body size, and presence of a nuchal crest and keeled vertebral scale line. Storr (1982), in resurrecting *Ctenophorus*, did not place *C. caudimaculatus*, *C. cristatus*, *C. mckenziei* or *C. scutellatus* in any of the species-groups within the genus. Subsequently, Storr *et al.* (1983) placed all four species together with the *C. reticulatus* species-group of Storr (1966) and *C. decreesii* species-group of Houston (1978) in a single expanded *C. decreesii* species-group, noting that this was merely an assemblage, and associated *C. mckenziei* and *C. scutellatus* in an undiagnosed informal subgroup, linked by inference (Storr *et al.* 1983: 32) with *C. cristatus*. Whitten (1982², 1985) placed *C. scutellatus* with the *C. maculatus* group and *C. cristatus* with *C. caudimaculatus* in a *C. cristatus* group. Both groups shared dark ventral markings and posterior interscalar femoral and preanal pores. The *C. cristatus* group was differentiated from the *C. maculatus* group by the more widely spaced pores, and smooth (vs usually keeled) ventral scales. The presence of a vertebral scale ridge and a nuchal ridge was considered diagnostic for the *C. cristatus* group, although the presence of both dark ventral pattern and a vertebral scale ridge in *C. scutellatus* was considered primitive within the *C. maculatus* group. A vascular tissue block deep to the vertebral and nuchal ridges, possibly functioning in crest erection, was noted for *C. cristatus* and *C. caudimaculatus*, but was not found in the *C. maculatus* group members examined (which did not include *C. scutellatus*). Crest erection was noted for *C. cristatus*, but not for *C. caudimaculatus*. We have observed nuchal crest erection in both *C. caudimaculatus* (G.M.S.) and *C. scutellatus* (M.P.; Storr *et al.* 1983, Plate 2). However, Whitten (1982) considered this vascular tissue block to be plesiomorphic within *Ctenophorus*.

Body, head and limb proportions are similar in *C. cristatus*, *C. mckenziei* and *C. scutellatus* (Table 1) and all share similar male ventral pattern, a nuchal crest, and a vertebral line of enlarged, strongly keeled scales, the latter unlike members of the *C. maculatus* species-group. Consequently, we believe that the affinities of

TABLE 2. Comparison of thermal preferences among three *C. mckenziei* run in a thermal gradient. Measurements are in °C.

Lizard	n	\bar{x}	σ^2	Range
R32267	129	35.3	2.43	29.2-39.9
R32268	151	34.4	3.44	11.1-39.0
R32269	138	34.5	4.05	13.0-43.4
Total	418	34.7	3.41	11.1-43.4

$F_{2,415} = 3.2667$, $p = 0.04$.

¹ MOODY, S. M. (1980) 'Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia)'. (PhD thesis, University of Michigan).

² WHITTEN, G. J. (1982) 'Comparative morphology and karyology of the Australian members of the family Agamidae and their phylogenetic implications' (PhD thesis, University of Sydney).

C. mckenziei and *C. scutulatus* are with *C. cristatus*, although it is clear that a more rigorous cladistic analysis of the phylogenetic relationships within the Australian agamid radiation is sorely needed.

Diet

The ant-dominated diet of *C. mckenziei* is similar to that reported for other small *Ctenophorus* species (Pianka 1986; Baverstock 1979; Mitchell 1973). Although *Iridomyrmex* spp. were the most commonly eaten ants, their dominance may simply reflect availability rather than any selection by the lizards (E. Matthews, pers. comm.).

Behaviour

The behaviour reported here for *C. mckenziei* has been observed in other species of Australian agamids. The hind-leg push-up display was thought by Gibbons (1979) to be unique to the *C. decresii* complex. The observations presented here show that this is clearly not the case. Whether this behaviour is homologous in *C. mckenziei* and the *C. decresii* group is unclear.

Thermal preferences

The mean body temperature of *C. mckenziei* reported here is lower than that reported for *C. scutulatus* in a laboratory gradient by Licht *et al.* (1966). It is unclear whether this is a real difference or an artefact of conditions which the animals experience during acclimation or while in the thermal gradient. It is noteworthy that Licht *et al.* (1966) used a thermal gradient in which the minimum temperature available was 25°C, considerably above the voluntary minimum body temperatures experienced by two of the three *C. mckenziei* tested.

While the observation that the voluntary maximum was recorded at night may at first seem unusual in an animal belonging to a group traditionally thought of as diurnal heliotherms, this is not really so. Several species of agamid are known to exhibit some nocturnal activity when thermal conditions allow (Fyfe 1981; Morley & Morley 1985; Bedford 1991; G.R.J., G.M.S., pers. obs.). A constant source of heat in a thermal gradient probably presents as near optimal conditions for nocturnal activity of agamids as possible. However, the low variance exhibited by *C. mckenziei* at night (1.86 vs 6.22) indicates that nocturnal activity is limited.

Comparative material examined (all localities in Western Australia)

C. cristatus: WAM R41827, 2 mi SW Wahlyamoning Rock; R68001-04, R68023-24, 4 km SW Lake Cronin; R68005, R68029, Lake Cronin; R68006, 2.6 km SW Lake Cronin; R68021-22, 5 km SW Lake Cronin; R70707, Frank Hann National Park; R71833, 19.5 km 78° Toomey Hills.

C. scutulatus: SAM R1459a-j, R3024a-b, R4814a-l (syntypes), between Fraser Range and Queen Victoria Springs; WAM R1235, R1761, Laverton; R2841, Gutha; R5306, Wadgingarra; R8170-71, "Yuin"; R9352, Malcolm; R9510, Morowa; R11236, Carnarvon; R12209, Shark Bay; R21865-67, Caron; R48385-89, 40 km N Beacon; R53551, 15 km E Point Sunday; R59605-06, 20 km ENE "Meadow" HS; R86769, 14 km WNW Mallee Hen Rocks.

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REPRODUCTION AND GROWTH OF THE SMOOTH PEBBLE CRAB *PHILYRA LAEVIS* (BELL 1855) AT TWO SITES IN SOUTH AUSTRALIA DURING 1990-91.

By **STEPHEN C. MCKILLUP*** & **RUTH V. MCKILLUP***

Summary

McKillup, S. C. & McKillup, R. V. (1994) Reproduction and growth of the smooth pebble crab *Philyra laevis* (Bell 1855) at two sites in South Australia during 1990-91. Trans. R. Soc. S. Aust. 118(4), 245-251, 30 November, 1994.

The growth and life history of the smooth pebble crab *Philyra laevis* (Bell) was inferred from collections made between July 1990 and December 1991 from Sultana Point and Coobowie, South Australia. *P. laevis* appeared to be semelparous and to reproduce twice a year at both sites. At Sultana Point ovigerous females were common in winter (June-July) and from late spring to late summer (November-February). Dead adults were common from late winter to early spring and also in early summer. Distinct cohorts of new recruits were found in early spring and again in early summer. Recruits grew rapidly, reaching sexual maturity within four months. The mean size of adult females and the proportion which were ovigerous differed amongst populations. A laboratory experiment showed that food availability affected growth and whether females became ovigerous. We postulate that differences in size and ovigery amongst populations of *Philyra laevis* may be caused by differences in the availability of food.

Key Words: *Philyra*, pebble crab, life-history, intertidal, food, sandflat.

REPRODUCTION AND GROWTH OF THE SMOOTH PEBBLE CRAB *PHILYRA LAEVIS* (Bell 1855) AT TWO SITES IN SOUTH AUSTRALIA DURING 1990-91.

by STEPHEN C. MCKILLUP* & RUTH V. MCKILLUP*

Summary

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KEY WORDS: *Philyra*, pebble crab, life-history, intertidal, food, sandflat

Introduction

The smooth pebble crab, *Philyra laevis* (Bell 1855), is common on sheltered intertidal sandflats in southern Western Australia, South Australia, Tasmania and Victoria (Phillips *et al.* 1984). Hale (1976) describes the feeding and courtship behaviour of *P. laevis*, but little else is known about this crab. Tasmanian populations of *P. laevis* have been reported to host a nemertean (genus *Carcinonemertes*) (Bell & Hickman 1985) and the trematode *Microphallus paragrapsi* Smith, 1983 (Bell 1988). From 1990-91 we studied the feeding behaviour of *Philyra laevis*, finding that although individuals often fed upon other dead or damaged animals, many were unwilling to feed upon members of their own species and that water borne cues from damaged *P. laevis* inhibited feeding (McKillup & McKillup 1992). During the study, we collected *P. laevis* over an 18-month period from two sites 10 kilometres apart in South Australia, and also sampled 10 other southern Australian sites. These data, together with results of a laboratory feeding experiment, are used to infer the life history of *P. laevis*.

Methods

Sampling of Philyra laevis from Sultana Point and Coobowie

Samples of *Philyra laevis* were collected from the intertidal sandflat at Sultana Point, lower Yorke Peninsula, South Australia (35.08°S 137.44°E) in July 1990, and then approximately every four weeks from September 1990 to August 1991 and in December 1991.

The sandflat at Coobowie Bay, 10 km north of Sultana Point, was sampled in the same way but less frequently (November 1990 and January, March, April, August and December 1991).

P. laevis is active whilst the sandflat is covered by water during ebb and rising tides, but remains buried in the substratum at high water or when the sandflat is completely exposed (Hale 1976). At least 30 and usually more than 100 individuals were collected from within the intertidal zone where *P. laevis* occurred (from low water to about mid tidal level) between the time of low water and when the sandflat was inundated by the rising tide. At each site at least 160 m² of substratum, consisting of several haphazardly chosen 0.5 metre wide strips from the water's edge to mid tide level, were hand searched to a depth of 3.5 cm. *P. laevis* was found no deeper than 3.0 cm in the substratum (McKillup & McKillup unpubl.). Crabs were frozen and later examined for sex, whether females were ovigerous, and the carapace width of all individuals was measured to the nearest 0.05 mm.

Reproductive condition and average size of adult females at additional sites

During January and February 1991, at least 75 *Philyra laevis* were collected from each of 11 sites in South Australia and one in Victoria (Swan Bay within Port Philip Bay), and examined for sex, size and reproductive state as described previously.

Laboratory experiment on sexual development and growth

Abdominal morphology in the Crustacea can usually be used to determine sex: adult males often have a relatively narrow, concave sided and tapered abdomen, whilst females have a broader and often circular abdomen almost as wide as the carapace (Hartnoll

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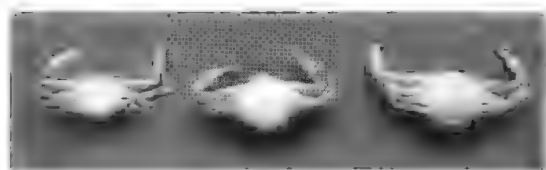


Fig. 1. Abdominal morphology of *Phillyra laevis*. From left to right: male, intermediate (= juvenile female) and adult female.

1982). This was the case for all *Phillyra laevis* with carapaces wider than 13.5 mm, but three morphological types were found in crabs 13.5 mm wide or smaller: the two previously described forms, plus individuals with a convex sided abdomen which, at its widest point, was approximately half the width of the carapace (Fig. 1). The last described individuals were named "intermediates".

The growth of 20 females, 20 intermediates and 20 males, all of carapace width 10.5 mm or less, was observed in the laboratory. Considering that we also found differences in the size and proportion of adult females which were ovigerous amongst sites, and that differences in adult size amongst (unspecified) localities were also reported by Hale (1976), observations were made as part of a manipulative laboratory experiment designed to examine the effects of food availability upon growth and egg production of *Phillyra laevis*. Crabs were placed individually in 50 x 50 x 30 mm deep plastic dishes, each filled with 40 ml of seawater. All individuals were numbered on the dorsal side of their carapace with non-toxic waterproof ink. Six dishes, containing two males, two females and two intermediates were placed within each of 10 lidded 280 x 380 x 110 mm deep plastic trays containing seawater to a depth of 10 mm. Aeration was not needed. The seawater in the trays maintained a high level of humidity which reduced evaporation from the dishes and also provided a marine environment for the few crabs which climbed out during the experiment. Trays were kept at room temperature and natural day length.

Five trays were assigned randomly to a "high food" treatment and the 30 crabs within these were fed every working day (from Monday to Friday), whilst the 30 crabs in the other five trays were fed weekly, on Wednesdays, as a "low food" treatment. Different frequencies of feeding provide different levels of food availability to invertebrates (e.g. Calow 1973; Moriarty 1978). For each feeding the six crabs in a tray were removed, placed in six separate dishes used for feeding only and offered *ad libitum* crushed cockle, *Kateleyia scalaris* Linnæus, from Sultana Point. *P. laevis* is often found feeding on this bivalve in the field (McKillop & McKillop 1992). All crabs fed for 12 min or less and were returned to their permanent dishes

after 15 min. This method of feeding prevented the seawater in the permanent dishes from becoming fouled; it was replaced fortnightly. Crabs were inspected on every working day, individuals which had moulted were examined and sexed as either male, female or intermediates, and any which had climbed out were replaced in their dishes.

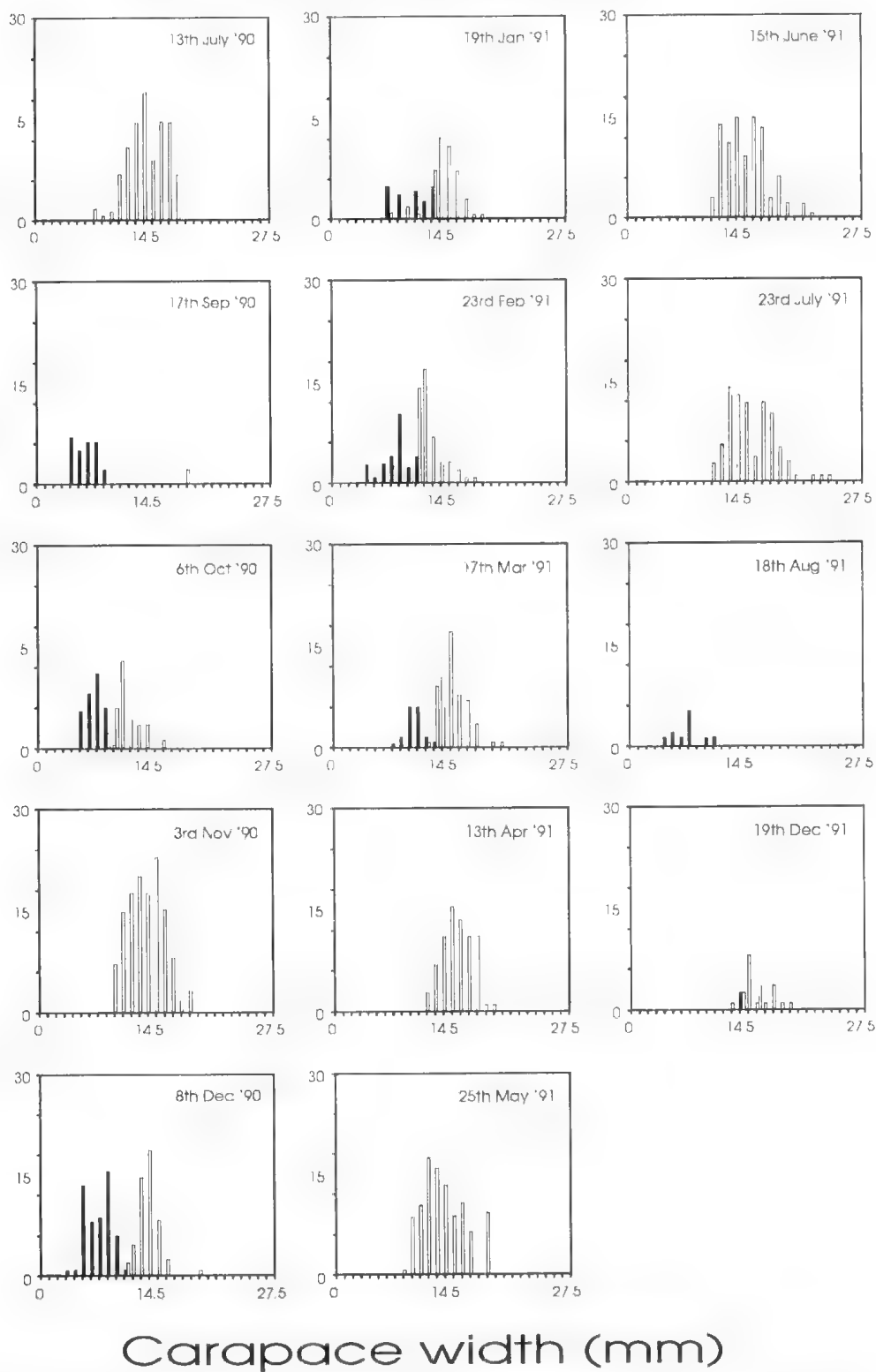
The experiment began on April 2nd 1991 using new recruits from the December 1990 - January 1991 cohort at Coobowie, and continued until all crabs had moulted at least once.

Results

Sampling of Phillyra laevis from Sultana Point and Coobowie

The size structure of the population of *Phillyra laevis* at Sultana Point from July 1990 to December 1991 is illustrated in Figs 2, 3. In mid-winter (July 1990), all males were at least 8.5 mm wide, all females at least 7.5 mm wide and 93% of the latter were ovigerous. By early spring (September 1990), dead males and females were extremely common and large live individuals were not: almost half of the live males collected were smaller than 8.5 mm and appeared to be a distinct cohort of recent recruits. Only two live adult females were found; both were more than 7.5 mm wide and ovigerous. The remainder of the sample consisted of "intermediates" 7.5 mm wide or smaller, which were not present in the July sample. A laboratory experiment showed that intermediates were juvenile females (see below). In mid-spring (October 1990) only one cohort of males was present, and these males were larger than the recruits first seen in the previous month. The juvenile females were also larger and some relatively small adult females were present, but none was ovigerous. In late spring (November 1990), no juvenile females were found; the sample consisted of adult females at least 9.5 mm wide, 89% of which were ovigerous, plus males from 4.5 to 18.5 mm wide. In early summer (December 1990) another cohort of relatively small males was present, together with a cohort of juvenile females up to 9.5 mm wide. Dead adults were again common, but live adults were also found and 71% of adult females were ovigerous. The small males and juvenile females continued to grow through summer and autumn (January to April 1991) and the number of ovigerous adult females declined (30.6% in January, 14% in February and 5.6% in March). From mid- to late-autumn (April and May 1991) no juvenile females were found and only 1.5% and 2% respectively of adult females were ovigerous, but in early winter (June 1991), the percentage of ovigerous females had risen to 68% and further increased to 94% by late winter (July 1991). The early spring (August 1991) sample was very similar to that of September 1990; dead adult males and

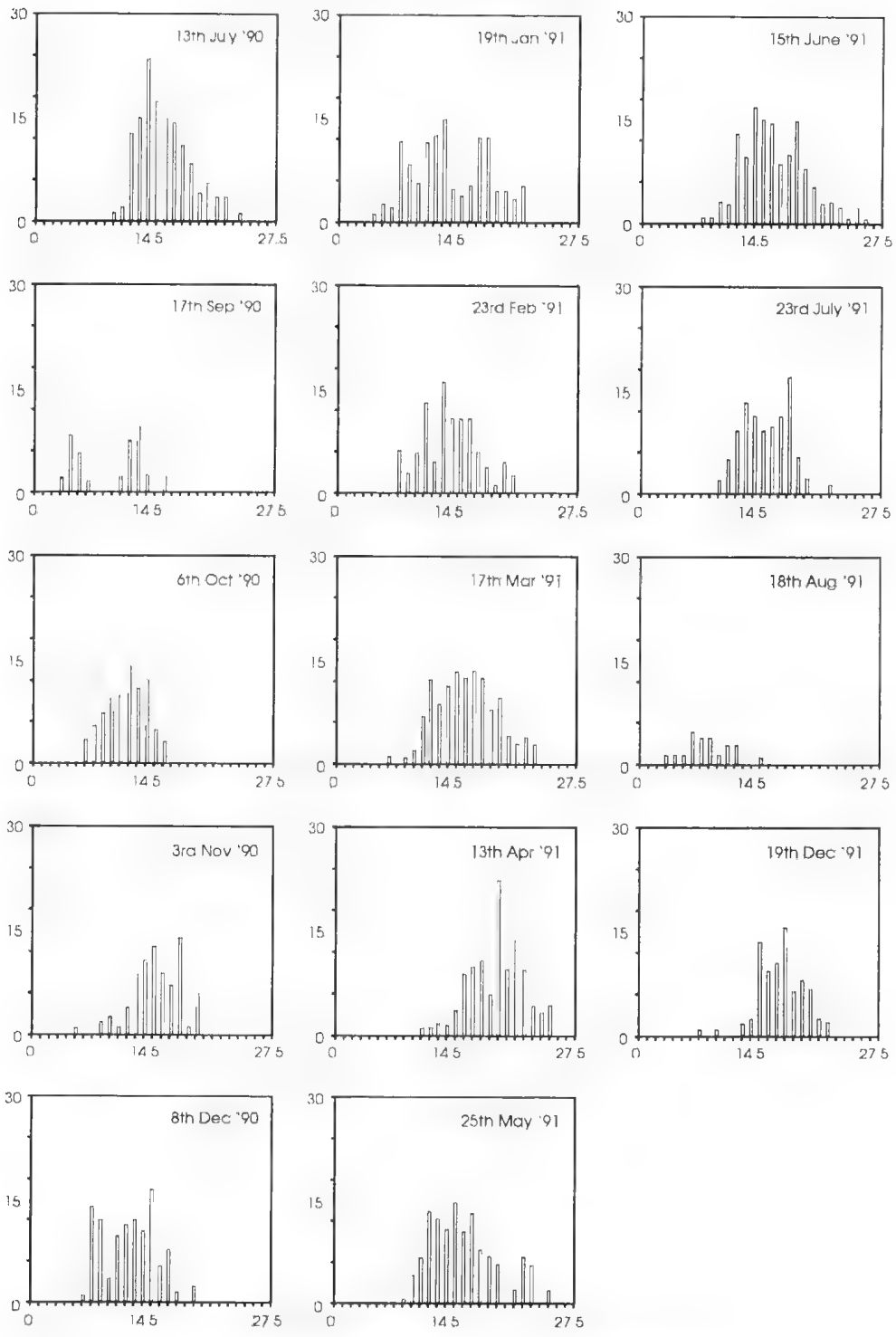
Number of crabs in each size class



Carapace width (mm)

Fig. 2. The size structure of female *Philyra laevis* collected from Sultana Point, South Australia on 14 occasions between July 1990 and December 1991. Solid bars indicate juveniles; open bars, adults.

Number of crabs in each size class



Carapace width (mm)

Fig. 3. The size structure of male *Philyra laevis* collected from Sultana Point, South Australia on 14 occasions between July 1990 and December 1991.

females were common and the sample of live *Philyra laevis* consisted entirely of juvenile females less than 8.5 mm wide and males which were almost all smaller than those collected during the previous month. The December 1991 sample was similar to the one from the previous December, consisting of adult males plus adult and some juvenile females, with 65% of adult females ovigerous. Dead adults were again common on the sandflat at Sultana Point in December 1991.

The data for Coobowie were consistent with those from Sultana Point. In late spring (November 20th 1990) only males and adult females were found, but in mid summer (January 19th 1991) juvenile females were also present and dead males and adult females were common. The average carapace width of the

cohort of juvenile females present in early autumn (March 17th 1991) was larger than in January and most appeared to have moulted to adults by April 13th 1991. In late winter (August 18th 1991) dead adults were common and juvenile females plus small males were present. In early summer (December 19th 1991) dead adults were also found, very few live adult females were present and juvenile females were common.

The mean carapace width of adult females was always greater at Sultana Point than Coobowie (Table 1) and a greater proportion of adult females was ovigerous at Sultana Point than Coobowie on five occasions when comparison was possible (Table 2). Males were not compared since it was impossible to distinguish between juveniles and adults.

TABLE 1. Comparison of the mean carapace width (in mm) of adult female *Philyra laevis* from Coobowie and Sultana Point. The November collections were made 17 days apart; on the other 5 occasions crabs were collected from both sites on the same day. \bar{x} = mean, s_x = standard deviation and n = sample size.

Date collected	n	Coobowie		Site		Sultana Point	
		\bar{x}	s_x	n		\bar{x}	s_x
November 1990	33	9.23	2.37	125		13.17	2.02
19 January 1991	17	12.74	1.75	49		13.19	1.73
17 March 1991	52	12.62	1.42	71		13.68	1.72
13 April 1991	85	13.18	1.75	65		14.19	1.77
18 August 1991	22	11.82	1.94			none found	
19 December 1991	9	11.72	1.72	22		13.50	1.83

TABLE 2. The number of adult female *Philyra laevis* and those ovigerous in samples collected from Coobowie and Sultana Point on 6 occasions during the same month. The November collections were made 17 days apart, on the other 5 occasions crabs were collected from both sites on the same day.

Date collected	Coobowie		Site	
	Collected	Ovigerous	Collected	Ovigerous
November 1990	33	1	128	119
19 January 1991	17	0	49	15
17 March 1991	52	0	71	4
13 April 1991	89	0	65	2
18 August 1991	22	15	0	-
19 December 1991	9	0	22	14

TABLE 3. The percentage of ovigerous adult female *Philyra laevis* at 12 sites sampled during January and February 1991, together with the mean carapace width of adult females from each site.

Date sampled	Site	Number of mature females collected	Number and percentage ovigerous	Mean carapace width of females (mm)
19 January 1991	Edinburgh Bay	9	0 (0)	12.67
19 January 1991	Sultana Point	49	15 (31)	13.19
19 January 1991	Coobowie	17	0 (0)	12.74
19 January 1991	Hickey's Point	25	2 (8)	13.10
19 January 1991	Stansbury	33	7 (21)	14.35
20 January 1991	Point Turton	3	0 (0)	14.83
20 January 1991	Rogues Point	86	6 (7)	13.90
29 January 1991	James Well	20	1 (5)	12.65
29 January 1991	Pine Point	23	1 (4)	12.33
2 February 1991	Frail Bay	87	0 (0)	13.89
2 February 1991	Sturt Bay	70	10 (14)	13.10
13 February 1991	Swan Bay (Vic.1)	66	56 (85)	17.46

Reproductive condition and average size of females at additional sites

Data for the number of adult females collected and the number and percentage which were ovigerous for 12 populations sampled in mid to late summer 1991 are in Table 3. The percentage of ovigerous females decreased at Sultana Point from January to February, so only samples collected on the 19–20th January 1991 were compared statistically. Nevertheless, the proportion ovigerous differed significantly amongst the seven sites sampled on lower Yorke Peninsula (2 x 7 contingency table comparison: $df = 6$, Chi-squared statistic = 22.26, $P < 0.005$). The significant heterogeneity amongst sites was largely due to the greater proportion of ovigerous females at Sultana Point (Table 3). Considering all sites sampled, the highest percentage of ovigerous adult females (85%) was at Swan Bay, Victoria during early February (when only 14% were ovigerous at Sultana Point; see earlier discussion of Figure 1). The Swan Bay population also contained the largest *Philyra laevis* found. Furthermore, for the seven sites sampled from the 19–20th January (excluding Point Turton where only three females were collected), ovigerous females were found only at sites where the average carapace width of females was greater than 13.00 mm (Table 3).

Laboratory experiment on sexual development

Male, adult female and "intermediate" *Philyra laevis* offered food on five of seven days per week moulted sooner than those only fed once per week (Table 4). At their first moult in the laboratory all males moulted to males, all females to females and all intermediates to females, except for the two smallest which remained as the intermediate form until they moulted again. In all cases the variance of days elapsing before moulting was greater in the low food treatment, and by inspection the distributions in this treatment were skewed to the right. None of the adult females in the low food treatment, but all in the high food treatment, were ovigerous by July 1991.

Discussion

Philyra laevis reproduced twice a year at Sultana Point and death of most adults during the breeding months suggests this species is largely semelparous. Recruits found in early spring, (September 1990)

reached sexual maturity and reproduced from late spring to late summer (November 1990 to February 1991), while those first found in early summer (December 1990) reached sexual maturity by mid autumn (April 1991) and reproduced until early winter (June 1991). Data from Coobowie were consistent with this pattern of recruitment, but suggest that many adult *P. laevis* at Coobowie did not reproduce in the summer of 1990–91, although data were scanty, being only for November 1990 and January 1991.

Recruits were found one month after reproducing females were present in late spring and two months after they were present in early winter. Considering that the sandflat was only sampled monthly, that the smallest crab found was 2.8 mm (McKillup & McKillup unpubl.) and that smaller individuals were likely to be overlooked amongst sand grains and detritus, the larval stage of *P. laevis* is likely to be of relatively short duration (perhaps only 1–2 weeks). Another member of the same genus, the purse crab *Philyra globosa* (Fabricius), has a larval stage lasting 11 days in the laboratory at an average temperature of 28°C (Krishnan & Kannupandi 1990).

The moult from juvenile to adult form in females appears to coincide with sexual maturity, since only two females with juvenile abdomens of more than 300 examined were ovigerous (McKillup & McKillup unpubl.). A relative ("non-allometric") increase in abdomen compared to carapace width during the moult to adulthood is common in brachyurans (Hartnoll 1974).

For sites sampled from the 19–20th January 1991, a greater proportion of ovigerous adult females was present where the mean carapace width of females was relatively large. Also, there was a greater proportion of ovigerous females at Sultana Point than Coobowie on all occasions when comparison was possible. Differences amongst sites were not caused simply by larger females being more likely to be ovigerous; examination of the data used to compile Table 2 showed that in November, 60 of 69 adult females between 8 and 13 mm wide were ovigerous at Sultana Point, but none of 19 collected on the same date and within the same size range was ovigerous at Coobowie. Furthermore, on January 19th 1991, none of the 17 adult females collected from Coobowie was ovigerous, even though the carapace widths of these individuals were

TABLE 4. The mean days elapsing before *Philyra laevis* first moulted in high and low food treatments. \bar{x} = mean, s_x = standard deviation, n = sample size

	n	Treatment			
		High Food \bar{x}	s_x	Low Food \bar{x}	s_x
Males	10	34.10	3.78	39.10	17.10
Females	10	23.5	7.38	45.20	25.31
Intermediates	10	22.10	10.79	38.10	21.81

within the size range of the 15 ovigerous females collected from Sultana Point. Similarly, on December 17th 1991, none of 9 adult females from Coobowie was ovigerous, even though six were within the size range of ovigerous females from Sultana Point.

Results of the laboratory experiment were consistent with food supply affecting the frequency of moulting. A sample of crabs will contain individuals at different stages of the moult cycle. In the low food group, crabs about to moult would have done so soon after the experiment began, but those which had moulted shortly before being collected would have to prepare to moult again under the laboratory conditions of low food availability. In contrast, in the high food group, crabs prepared to moult would do so, and others which had recently moulted would have adequate resources available to grow and moult again. This can explain the greater mean, variance and positive skew of the number of days before moulting in the low compared to the high food treatment (Table 4).

We suggest, for the following reasons, that differences in size and the proportion of ovigerous adult females amongst sites were caused by differences in food availability. Firstly, in the laboratory, crabs in the high food treatment moulted sooner (and therefore grew faster) than those in the low food treatment, and only females in the high food treatment produced eggs. Secondly, adult female *P. laevis* at Coobowie were consistently smaller than those at Sultana Point. The intertidal scavenger *Nassarius pauperatus* (Lamarck), a prosobranch snail which occupies a similar niche and is often found feeding with *Philyra laevis*, is also smaller (and hungrier) at Coobowie than at Sultana Point, and we have postulated there is less food

available to *N. pauperatus* at Coobowie than at Sultana Point (McKillop & Butler 1979, 1983; McKillop 1983). Furthermore, we have more recently postulated that intertidal scavengers may generally be short of food (McKillop & McKillop 1994). All South Australian populations of *P. laevis* sampled contained smaller females on average than the population at Swan Bay Victoria, suggesting that food availability may be limiting the growth and reproduction of many populations of this scavenger. Notably, females of another leucosiid crab, *Ehulia laevis* (Bell, 1855) were only found ovigerous during December, January, May and August at Wellington, New Zealand, but records from other localities suggest the duration of the reproductive season varies amongst sites (Wear & Fielder 1985).

The hypotheses that differences in food availability are limiting the duration of the reproductive period of *Philyra laevis* and that individuals in natural populations of this species are short of food could be tested by frequently feeding marked individuals in the field and comparing their growth and reproductive output with the rest of the population. The results of these experiments may explain why *Philyra laevis* has a relatively short lifespan and two seasonally opposed breeding seasons in South Australia.

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THE HISTORY OF THE DEVELOPMENT OF THE PACIFIC OYSTER, CRASSOSTREA GIGAS (THUNBERG) INDUSTRY IN SOUTH AUSTRALIA

*BY A. M. OLSEN**

Summary

Olsen, A. M. (1994) The history of the development of the Pacific oyster *Crassostrea gigas* (Thunberg) industry in South Australia. Trans. R. Soc. S. Aust. 118(4) 253-259, 30 November, 1994.

The dredge fishery for the native mud oyster *Ostrea angasi* Sowerby in South Australia had a chequered history before finally collapsing in 1945. Attempts to cultivate the native oyster on leases were only partially successful. The importation of seed oysters of the Pacific oyster *Crassostrea gigas* from Japan in April 1970 by a private company began the successful aquaculture of this rock oyster. The aquaculture of the Pacific oyster has filled the market niche left by the loss of the mud oyster fishery.

The background history of the several introductions of seed oysters (spat) from Japan, Tasmania and Scotland is described.

Key Words: Pacific oyster, *Crassostrea gigas*, history, introduction, South Australia.

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Introduction

From the early days of the colony, oysters were being marketed from beds on the western side of Gulf St Vincent and the northern side of Kangaroo Island. By 1871 the dredge fishery was concentrating on oyster beds in Kellidie Bay where 30 sailing vessels employing 80 men were dredging 60 thousand bushels of oysters a year. Overfishing of the stocks occurred and by the late 1880s the fleet moved to new beds near Stansbury. Within a few years these beds were also depleted and the few remaining vessels moved back to the Eyre Peninsula beds so that by 1905 the mud oyster fishery had virtually collapsed. Over the next 25 years, when old beds showed signs of recovery boats entered the fishery only to leave later. In 1945 the mud oyster fishery ceased to exist (Olsen and Priest 1971; Wallace-Carter 1987).

Attempts to cultivate the native oyster at Stansbury and Kellidie Bay were only partially successful with the output limited by low recruitment. Mud (incubatory) oysters have a low fecundity compared with that of the mass spawnings and spat settlement of the rock (non-incubatory) oysters such as *Saccostrea commercialis* (Iredale and Roughley), the commercially important Sydney rock oyster and the introduced Pacific oyster *Crassostrea gigas*.

Early attempts to grow rock oysters in southern Australia

An attempt in 1886-7 to acclimatise the Sydney rock oyster at Hobart, Tasmania was unsuccessful (Saville-Kent 1887). A trial shipment of the same species spread

out on trays at Kelso, River Tamar, in northern Tasmania in 1948 by a Sydney rock oyster grower failed too (Olsen 1965).

In 1933-4 attempts were made to cultivate young Sydney Rock oysters on a commercial scale in South Australian waters. 228,000 oysters were laid out on trays off the west bank of the Port River below the Osborne Power Station where an earlier experimental consignment had reportedly grown very fast (Anon. 1934¹; Wallace-Carter 1987). Other attempts to acclimatise the Sydney rock oysters were made in 1937 at Mt Dutton and Kellidie Bays without success.

A small consignment of juvenile Sydney rock oysters from a warm water environment at a solar saltfield at Port Alma, Queensland was transferred in May 1976 into seawater of approximately similar salinity and temperature of the primary pond of the solar saltfield at Dry Creek. Within 3 months 95% of the experimental consignment died. Later the same year a second experimental consignment was transferred from the same source and these oysters suffered 70% mortality within a month. As a result of these experiments further translocation experiments into quarantine areas at Dry Creek ceased (Melvin per comm.).

So far as the author is aware the last attempt to acclimatise Sydney rock oysters in South Australia was in 1977 when oysters put into the commercial prawn farm ponds at Port Broughton failed.

Thomson (1952) remarked that conditions of the waters of the southern states are outside the natural range of the Sydney rock oyster.

When CSIRO Division of Fisheries and Oceanography imported Pacific oysters from Japan between 1947 and 1952, the author assisted with their establishment and supervision and, in September 1953, the transfer of the majority of the surviving stock to Port Sorell. It was on the basis of this experience that

* 11 Orchard Grove, Newton, South Australia. 5074

¹ ANON. (1934) Large scale farming of Sydney rock oysters in Port River. "The Saturday Mail" 14 July, 1934.

the author in 1968 considered the aquaculture of the Pacific oyster would be successful in South Australia. The Pacific oyster was already established as a viable reproducing stock on the rocky foreshore of the River Tamar near Sidmouth in Tasmania (Thomson 1959). By 1964 the Tasmanian authorities were granting leases for its commercial production. (Fig. 1)

At its January 24, 1968 meeting, the Flora and Fauna Advisory Committee, a body responsible to the Minister for Agriculture, South Australia, examined a proposal from the Director of Fisheries and Fauna Conservation Department for Pacific oysters to be introduced from Tasmania for aquaculture in South Australian waters. It was argued that the Tasmanian stock was disease-free and its introduction could fill a niche no longer occupied by the native mud oysters. The Committee did not raise any objections to the recommendation. The Department itself did not have the staff or funds to undertake the import and establishment of the Pacific oyster but wanted to be able to encourage private enterprise to do so.

In June 1968, J. T. Belling of Balaklava asked the Department whether an oyster lease, currently held by W. Lee of Kellidie Bay, could be transferred to another company of seven shareholders who wished to expand production of the native mud oyster. There was no objection and subsequently Oyster Farmers Coffin Bay Pty Ltd was registered as lessee of the Kellidie Bay oyster lease.

Later in the year two Adelaide men, C. J. Mack and R. C. Sprigg, also approached the Department about

obtaining leases for experimental oyster production. The author suggested they meet J. T. Belling to discuss the problems associated with cultivation of mud oysters. He also suggested that they might like to combine and import a consignment of Pacific oysters from Tasmania. The group was advised to visit Wivell Bros' Tasmanian Rock Oyster Company at Sidmouth, River Tamar, to see the techniques used there and to find out about the transport of oysters to Adelaide. After a visit by the men to Wivell Bros in March 1969, an order was placed with the company for 50 bags, each containing about 120 adult oysters for delivery to South Australia in September 1969.

After their return, arrangements were made with R. C. Sprigg's organisation, Geosurveys Pty Ltd for its workshop to make and tar oyster trays. Tared trays were taken to Sprigg's site at Coobowie and Mack's at Kangaroo Island which had been preselected so that the trays could be attached to stakes, above the sea floor, but situated below water level at low tide.

The 15 bags purchased for Mack's lease were set out above a seagrass bed (*Zostera muelleri*) at 0, 1 and 2 m below low water near Picnic Point, American River, Kangaroo Island and Sprigg's were set out below low water off the Coobowie Marine Research Station, Yorke Peninsula. The remaining 20 bags were taken by truck and laid out on the Oyster Farmers Coffin Bay Pty Ltd lease at Kellidie Bay, Eyre Peninsula. The adult oysters all acclimatised and grew well. Although they spawned three months after being set out no spat settled at or near any of the three leases.

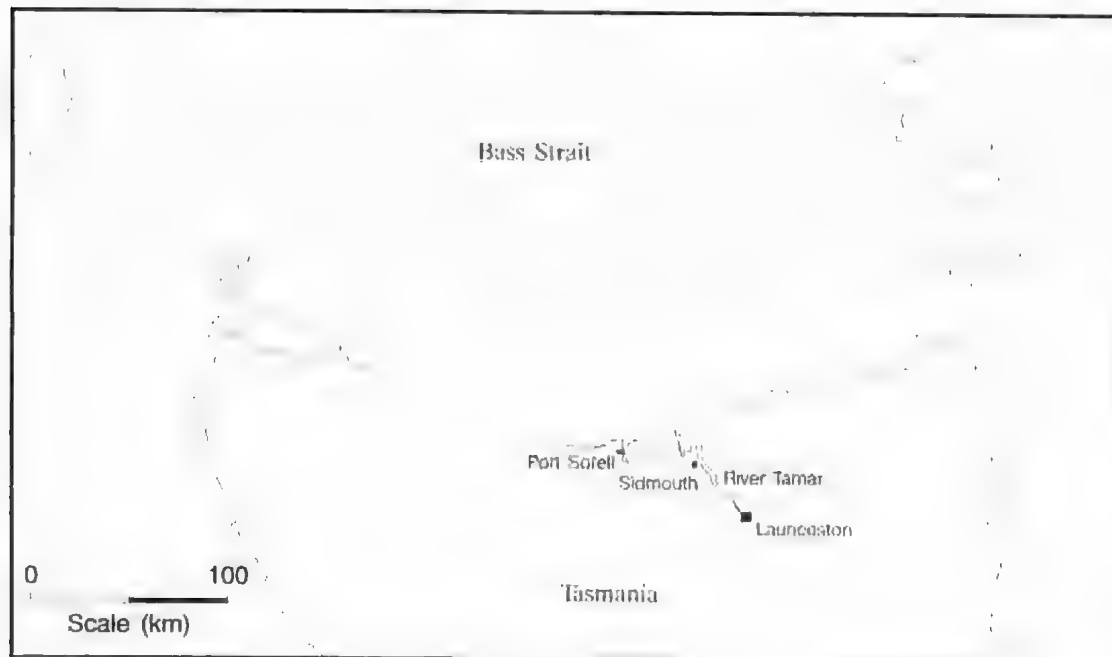


Fig. 1. Locations in Tasmania of spawning wild populations of Pacific oysters.

Environmental conditions including high salinities (35 ppt) must have been inimical to the survival and settlement of larvae of the Pacific oyster. Many commercial hatcheries operate at salinities of 32-34 ppt or even 36 ppt and salinities of 30-34 ppt are reported from seed-producing areas in Japan and from areas of France where *C. gigas* reproduces successfully (Coleman, 1986). However, continuous exposure to salinities greater than 32 ppt is lethal to Pacific oyster larvae and according to Medcof and Wolf (1975) this is the reason there has been no spat fall in Coffin Bay, South Australia.

The sustained growth and excellent condition of the imported adults on the Oyster Farmers lease prompted the Company to consider importing Pacific oyster seed (spat) by air from Japan. One of the shareholders, who wrote and spoke Japanese fluently, flew to Japan to examine cultivation techniques first hand. While at Sendai, Miyagi Province, he sought details of air-freighting oyster spat to Adelaide. Full details of quality, quantity and costs from Sendai to Adelaide were received on February 23, 1970.

Importation of seed oysters (spat)

In early March an application to import a trial shipment of spat by air from Japan was lodged with the Chief Quarantine Officer (Animals), South Australia. Permission to import the spat was received on March 24, subject to compliance with all quarantine requirements. A 19 kg box containing 6000 Grade A unbroken oyster spat was ordered to be air-freighted to Adelaide and was received on April 12. Some minor problems with quarantine requirements were resolved quickly and the spat was released in good condition from quarantine on April 28 and set out on the Kellidie Bay lease.

A second application from Oyster Farmers Coffin Bay to import 100,000 certified disease-free oyster spat by air from Mitsui and Co. Ltd., Sendai, was lodged with the Department of Health, Canberra in August 1970 (Fig. 2). This was cheaper than buying and transporting the spat by sea from Tasmania.

In the second application the company wrote "the growth rate of this 1970 seed is proving to be excellent and we, therefore, wish to further our experiments with the rate of growth for production with view to sale. It is anticipated that 100,000 seed be imported in 1971 with follow-up quantities as and when considered appropriate. Our next consignment will be by air, however, we request permits to cover both AIR and SEA transport so that seed mortality during transit may be compared."

The application was refused by the Commonwealth-States Advisory Committee in February 1971. The

grounds for refusal were never made known despite a request for such from the South Australian Department. The introduction of certified disease-free oyster spat direct from Japan to South Australia did not pose a disease threat to the NSW oyster but the development of an oyster industry did pose a potential competitor for the NSW commercial oyster monopoly.

After the refusal to allow spat to be imported from Japan, Oyster Farmers Coffin Bay ordered 2000 "sticks" from Wivell Bros. These "sticks" are milled stakes 2 metres long and 25 millimetres square. It was indeed fortunate that when the mass spawning of Pacific oysters from the higher trays occurred between January 26 and February 12, 1971, Wivell Bros had put out 87,000 tarred and cured "sticks". Consequently they had ample "sticks" to supply the order. A quantity of scallop shells (*Pecten alba*) were set out also as an alternative cultch material (Wivell pers. comm.).

In April, 1971, Oyster Farmers Coffin Bay received 2000 "sticks" holding 120,000 spat oysters along with a quantity of scallop shells averaging 15 spat/shell. The shell sample was included to see if transport costs could be reduced by using this alternative cultch material.

The following year another consignment of 800,000 spat on scallop shells was received on April 20. The 1971 spat oysters continued to flourish and by December 1972, the spat had reached commercial oyster size and were sold (Reschke 1972²). There was a ready local market for these 11 month old oysters and Pacific oysters from McIntyre's Stansbury lease were also being marketed. He had obtained his 1971 spat from Wivell Bros, Sidmouth.

In early 1972 a tentative order for Pacific oyster spat was received by Wivell from a Welslipool (Victoria) buyer. However, the order was cancelled later when permission to import into Victoria was refused on the grounds of possible transmission of diseases (Wivell, pers. comm.) although no disease had appeared in 1955 when a large number of Pacific oysters had been transferred by the Victorian fisheries authorities from Pittwater (Tasmania) to Mallacoota Inlet. After three years 74,000 oysters were still alive but there was no evidence of any spat fall (Thomson 1959).

Disaster, however, struck the Tamar River oyster industry in 1973 when there was virtually no spat fall at any of the recognised settlement areas in January-February that year. It is believed that higher salinities at the leases resulted in poor gonad development following a prolonged dry spell - the longest on record (Wivell pers. comm.). The lack of freshwater flows in the Esk tributaries of the River Tamar allowed marine water from Bass Strait to penetrate further into the estuary during the long dry spell. The developing South Australian oyster industry, dependent on spat from Tasmania, was halted as the 2 million spat order for April 1973 could not be filled.

²RESCHKE, W. (1972) The oystermen of Coffin Bay. "Sunday Mail" 22 April, 1972.

Oyster Farmers Coffin Bay attempted to produce their own spat for on-going operations with a small scale industry operation but were unsuccessful because of difficulties in providing suitable algal food for the developing larvae.

About the same time that advice was received that no Tasmanian spat were available, the SA Department of Fisheries received an enquiry from Pacific Aquaculture Pty Ltd, a company holding an oyster lease in southern Tasmania, about the feasibility of growing Pacific oysters on long lines in South Australian waters. It also raised the possibility of establishing a co-operative venture hatchery in South Australia to remove the dependency on spat derived from a wild population in the River Tamar. The Department arranged a meeting between representa-

tives of this company and Oyster Farmers Coffin Bay. A beneficial outcome of this meeting was that Pacific Aquaculture had been granted permission to put down two experimental long lines seeded with oysters from their Tasmanian lease. One long line was located off Streaky Bay near Boston Island and the other in Proper Bay, west of Horse Rock, Port Lincoln. The subsequent growth of these oysters was excellent and by October, 1974, they averaged 7 cm in length. As the oysters grew their added weight dragged longline floats underwater until the bottom section lay on the sea floor. Starfish then attacked the oysters and about 10% were lost. Arrangements for additional flotation to be added, as needed, had broken down and the interstate company did not proceed any further with its longline experiments.

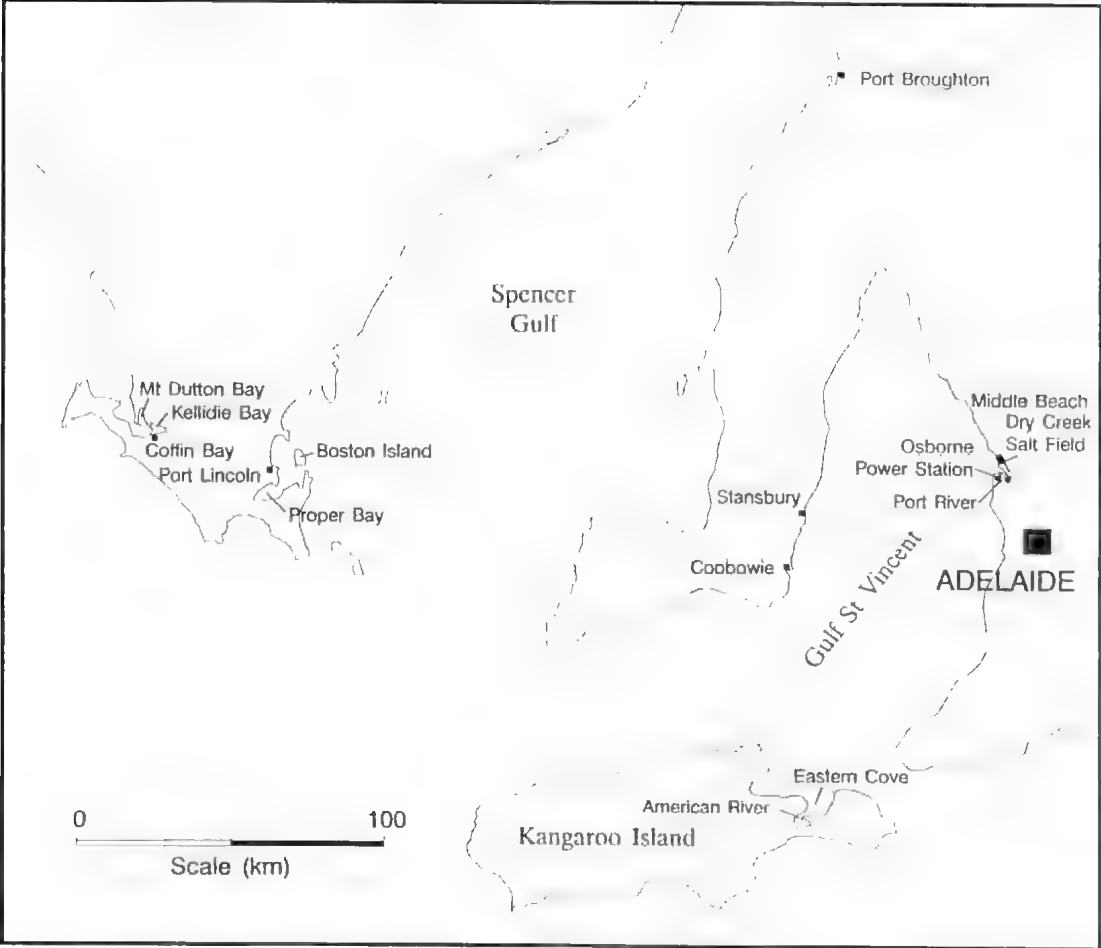


Fig. 2. Locations where attempts were made to grow introduced rock oysters.

From 1968 the Department of Fisheries had been involved in surface and ecological studies and more recently it had carried out similar studies under contract to other government departments and agencies. In late 1973, M. V. Melvin, Senior Production Officer, Alkali and Chemical Group, ICI, approached the Department to undertake for ICI a contract ecological survey of the large 3 km² primary pond of the solar salt evaporation complex at Dry Creek. He was examining the feasibility of a multipurpose use of this pond for aquaculture of the western king prawn, *Penaeus lousideanus* or any suitable fish species (Reschke 1977¹). This primary pond ranges from 1.5 to 2.5 metres in depth, it is non-tidal and hypersaline (annual mean salinity of 40.9 ppt).

An ecological study lasting two months undertaken in January-February 1974, showed that the pond could be suitable for an aquaculture use (King 1974). The author advised ICI against the aquaculture of prawns or fish because of predation by birds but rather to consider the cultivation of the Pacific oyster *C. gigas*. The recommendation was based on the successful establishment of reproducing stocks of the mussel *Modiolus inconspans* and the cockles *Karrlysia* spp. as well as the general high productivity of other biota in the pond. The recommendation was accepted by the Board of ICI. M. V. Melvin ICI and M. G. King, Department of Fisheries, were to be responsible for a co-operative study of growing Pacific oysters in the primary pond. Preliminary experiments were started with oysters from Oyster Farmers Coffin Bay while awaiting delivery of spat ordered from Tasmania. There was, however, a failure of the January-February 1974 spat settlement but with an out-of-season March spawning, Wivell Bros were able to fill the ICI order with spat settled on scallop shell cultch. The spat of 19 mm mean size were delivered and set out in the pond on July 4, 1974.

A small central hole had been punched in each cultch shell, enabling it to be threaded on a length of 3 mm diameter galvanised steel wire (ren). Nine to 12 cultch shells each carrying one to nine oysters were strung on each wire ren and separated by 10 cm lengths of plastic hose. These rens were hung from fixed wooden racks at three positions in the pond. By May 1975 growth averaged 15 g/month. The spat had a mean net weight of 2.1 g when placed in the pond and grew to a mean wet weight of 97.3 g in 9 months. King (1977) reported an acceptable market size of 70 g was attained after being in the pond for 8 months or within approximately 1 year of settlement.

Because of the success of the initial experiment with growing Pacific oysters in the primary pond, ICI in

mid 1975 approved a submission for funds for an on-going program for Pacific oysters in the primary pond at the Dry Creek salt fields. An order for 30000 scallop shells averaging 8 spat/shell and 5000 "sticks" averaging 40 spat/shell was placed with Wivell Bros. The consignment shipped from Burnie, Tasmania, arrived in Adelaide on July 25, 1975 and was planted out at selected positions in the pond (Melvin 1977).

By now there was a growing awareness of a developing South Australian oyster industry. At Stansbury, J. McIntyre, who had been cultivating the mud oyster, *Ostrea angasi*, on his lease since about 1961, switched some of his cultivation to Pacific oysters in 1971. In April, 1975 B. Frankham, Henley Beach, Adelaide, put out scallop cultch shells with spat from Wivell Bros on longlines in his deepwater lease at Eastern Cove, Kangaroo Island (Tilbrook 1977²). As Frankham was being advised by M. G. King, Department of Fisheries, he did not repeat the mistakes with flotation experienced earlier by Pacific Oyster Aquaculture at Port Lincoln.

The highlight of 1975 regarding the cultivation of Pacific oysters in South Australia was the success of an application by Director of Fisheries to the Government for the appointment of an oyster biologist experienced in oyster hatchery production. Dr. B. O'Sullivan from Carna Research Station, Galway Bay, Ireland was appointed to this position and arrived in Adelaide in March 1977.

In January 1976 ICI, on the recommendation of M. V. Melvin, brought Dr. D. B. Quayle, a Canadian oyster biologist and world authority on the cultivation of Pacific oysters to report on the new developments at Dry Creek saltfields. He was impressed by the growth of the Pacific oysters in the unusual environment of the primary pond of a solar salt field, an environment not previously considered to be suitable for oyster cultivation. Dr. Quayle provided practical advice on cultivation and harvesting techniques at Dry Creek.

There had been a number of approaches in the previous two years to the SA Government to support the building of a local hatchery for Pacific oysters to remove the dependency on spat derived from wild populations in Tasmania. There were two occasions, 1973 and 1974, when there was no spat settlement from the Tasmanian January-February spawnings.

Because of the unreliability of supplies of spat from Tasmania, M. V. Melvin had considered alternative sources of spat. On October 20, 1976 ICI submitted an application to import 50000 cultchless spat of Pacific oyster from Scottish Sea Farms, Connell, Argyll, Scotland through the Minister of Fisheries, SA. This Scottish company was supplying certified disease-free cultchless oyster spat to buyers in Europe and South Africa. The parents of this source of spat were 6 adult Pacific oysters from Pendrill Sound,

¹ RESCHKE, W. (1977) Here's news to rock those Sydney oysters. "Sunday Mail", 6 February, 1977.

² TILBROOK, K. (1977) Down on the oyster farm. "Advertiser", 29 January, 1977.

British Columbia, Canada, imported by the Ministry of Agriculture and Fisheries Shellfish Culture Unit at Conway, Wales in June 1964. A year after the Minister had forwarded the ICI application, he was advised that the Advisory Committee on Import and Export of Live Fish of the Australian Fisheries Council had recommended that the proposal be approved. Another 12 months elapsed before formal written approval was received. There had been a rigorous examination by Commonwealth Quarantine and Department of Health authorities before permission to import cultchless spat from Scotland was granted. On arrival the spat were subjected to detailed quarantine inspection procedures and a period in quarantine. During the 2 year waiting period for approval to import spat, the 1977 River Tamar spat fall was a commercial failure with only 2 spat/scallop shell and 18 spat/"stick" being caught. This was the third failure in four years and highlighted the need for alternative sources of spat.

Early in 1977, a depuration unit was constructed and installed at Dry Creek. This apparatus used recirculated sea water, sterilised by irradiated UV light, to flush the gut of oysters. Oysters of marketable size were removed from the pond, separated from each other, cleaned externally with a jet of sea water and placed in the depuration unit where they remained for two days. This process was designed to prevent outbreaks of food poisoning such as had occurred in Victoria in 1975 and which had been attributed to infected NSW oysters. A trial marketing survey conducted in 1978 indicated a ready acceptance of the treated oysters. There were no requirements for depuration treatment of NSW commercial oysters until 1978-79 when it became mandatory following an extensive outbreak of food poisoning in that state from local oysters.

As a consequence of a favourable report from Dr Quayle after his Australian visit and the successful marketing of Pacific oysters from the primary pond, the Board of ICI approved M. V. Melvin's recommendation to build an oyster hatchery for Pacific oysters at Dry Creek. A draft agreement covering joint participation by ICI and SA Fisheries Research Branch in the design, commissioning and operation of an oyster hatchery at Dry Creek was received from the Board of ICI in March 20, 1978. Shortly after the agreement was signed on May 2, 1978, ICI advised that they had appointed Colin Palm, a Project Engineer with ICI, to be responsible for the design and construction of the hatchery through to commissioning. He was to be assisted throughout by his colleague, M. V. Melvin and B. O'Sullivan, the latter representing the SA Fisheries Research Branch of the now amalgamated Department of Agriculture and Fisheries. These three men brought chemical engineering and biological expertise to the design of the hatchery. Each aspect of the design and operation was carefully studied and operational difficulties were identified and where

possible either eliminated or reduced (Anon 1980). Copper, zinc, lead and their alloys were excluded from any contact with larvae or spat in the hatchery operations.

The 50,000 cultchless spat from Scotland, packed in mesh bags surrounded by damp newspaper to maintain a humid environment, arrived in Adelaide on September 14, 1978 in a polystyrene container. The spat were immersed in chlorinated fresh water for a few minutes and then rinsed in fresh water under supervision of quarantine officers before being set out on trays in the modified depuration unit. Water from the primary pond was pumped directly through the unit and discharged back into the pond for the quarantine period. The polystyrene container and newspapers were burnt under supervision.

Because of the failure of the 1977 Pacific oyster spat fall in Tasmania and the desire to maintain continuity of supply of adult oysters the Tasmanian fisheries authorities requested a permit to import one million cultchless oyster spat from Scottish Sea Farms. Permission was refused on the grounds that quarantine facilities in Tasmania were inadequate compared with the stringent conditions imposed at Dry Creek, South Australia.

It took only six months from the signing of the joint agreement in May until the designs of the building and equipment and the layout were approved in November, 1978. Seven months later the building was erected, equipment installed, tested and ready for commissioning. A fortnight later adults were brought into the hatchery from the primary pond for conditioning for spawning when required. At the same time the culturing of the algal food species for feeding the larvae and spat began. The first batch of one million oyster spat (1 mm in size) was placed in the pond on October 2 (Melvin 1979). They were expected to be ready for sale a year later after the depuration treatment. Batches in excess of one million spat were produced regularly thereafter (Olsen 1981).

In 1977 ICI Saltfields began an expansion program of the solar evaporative pond complex with the construction of a large impoundment at Middle Beach north of its original lease. New and more powerful pumps were installed to draw water from Gulf St Vincent. It was planned to incorporate the primary pond into the chain of ponds of increasing salinities.

By 1980 pumping of seawater into the primary pond from Chapman Creek was reduced and the new Middle Beach pond became the primary pond of the solar salt evaporative pond complex. Salinities in the former primary pond rose slowly to the required production level and consequently altered the long-established equilibrium environment there. Much of the biota identified in the January-February 1974 ecological survey failed to adapt to the water quality and salinity regimes. Thus the food of the oyster spat began to

decline as did the rate of growth of the oysters.

Coincidentally with this expansion of the production of solar salt was the widespread Australian drought. As a consequence of the drought conditions and lowered demand for agricultural chemicals and other products manufactured by ICI, the Board of ICI decided on a restructuring program of its Australian activities and to concentrate on production of its core products. It decided to withdraw from and close down its many diversified projects whether profitable or not. In 1983, the South Australian solar saltfield complex at Dry Creek was sold. The production of oyster spat ceased and the hatchery equipment was sold.

Fortunately for the developing South Australian oyster industry a new hatchery at Bicheno, Tasmania had come "on stream" in June 1981 so that the industry was no longer dependent on spat from the wild population of Pacific oysters in the River Tamar.

The success of the early aquaculture of Pacific oysters on leases in Kellidie Bay, Kangaroo Island,

Stansbury and in the original primary pond of the solar saltfield complex at Dry Creek stimulated the demand for leases for aquaculture of Pacific oysters. Initially there were 98 approved leases but when fees were introduced in 1992 this number dropped to 82. The present active, vigorous aquaculture of Pacific oysters in SA stems from the efforts and close co-operation between the fishery authority, three private individuals and one of the staff and resources of a large industrial manufacturing organisation.

Acknowledgements

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**STUDIES ON APRUTIDES GUIDETTI
(NEMATODA: SEINURIDAE) ISOLATED FROM SOIL
AT NORTHFIELD, SOUTH AUSTRALIA**

BY ALAN F. BIRD & GREGOR W. YEATES†*

Summary

Bird, A. F. & Yeates, G. W. (1994) Studies on *Aprutides guidetti* (Nematoda: Seinuridae) isolated from soil at Northfield, South Australia. Trans. R. Soc. S. Aust. 118(4), 261-266, 30 November, 1994.

Aprutides guidetti, originally described from Italy and subsequently from Turkey, was isolated from a heavy clay soil from Northfield, South Australia, where it comprises a major part of the soil nematode population. Only females have ever been detected and these have been examined and photographed alive under the light microscope. They have also been examined and measured under the light microscope after fixation and, after sectioning, under the electron microscope. This is the first record of this nematode in Australia.

Key Words: *Aprutides guidetti*, Seinuridae, soil nematodes, structure, taxonomy.

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KEY WORDS: *Aprutides guidetti*, Seinuridae, soil nematodes, structure, taxonomy

Introduction

During an examination of the number and diversity of nematodes from three different soil types in South Australia in the spring of 1992 (Yeates & Bird 1994) it was observed that a clavate-tailed aphelenchoid was the most common nematode in the black earth (Vertisol) of Northfield making up 19% of the total nematode population. This nematode was not observed in the red brown earths (Alfisol) of Kapunda and represented only 0.4% of the solonised brown earth (Entisol) of Avon and then only from land occupied by native shrubs. Because of its relatively large numbers in the Northfield site we have attempted to identify it using light and electron microscopes.

In this paper we show that the nematode from Northfield closely resembles the aphelenchoid *Aprutides guidetti* first described by Scognamiglio (1974) in Italy and later by Saltukoglu *et al.* (1976) in soil samples taken from grassland in the Kartal Maltepe, Camlica and Göztepe areas around Istanbul in Turkey.

We are confident that the clavate-tailed nematode from Northfield is *Aprutides guidetti* and have provided further information to establish its identity.

Materials and Methods

Nematode

A nematode subsequently identified as *Aprutides guidetti* was isolated by means of a misting apparatus from soil collected at Northfield, South Australia, from which this nematode had previously been extracted (Yeates & Bird, 1994).

Light microscopy

Nematodes were examined under bright field, phase contrast and differential interference contrast optics using a Vanox Olympus AHB research microscope. Living nematodes were examined in distilled water under a coverslip sealed at its edges with nail varnish and photographed using Ilford Delta 400 film. Specimens were fixed by adding an equal volume of boiling double strength FA 4:1 (20 ml 40% formaldehyde and 2 ml glacial acetic acid in 78 ml distilled water) to a shaken suspension of the nematodes in distilled water. These specimens were processed to pure glycerol by Seinhorst's (1959) method and mounted in anhydrous glycerol on slides sealed to a coverslip by molten paraffin as described by De Maesseneer & D'Herde (1963). Fixed nematodes in glycerol were photographed with Ilford Pan F film.

Electron microscopy

Specimens were picked out with a mounted eyelash and fixed in cold (4°C) phosphate buffered (pH 7.3, 0.1M) 4% paraformaldehyde, washed, fixed and stained in 2% aqueous osmium tetroxide, washed, dehydrated in ethanol and embedded and polymerized at 60°C in TK3 resin as previously described in more detail (Bird & Ryder 1993).

Sections were cut with a diamond knife in a Reichert-Jung Ultracut E ultramicrotome, mounted on uncoated grids and stained with aqueous 2% uranyl acetate followed, after washing, by 0.5% lead citrate in 0.1M sodium hydroxide as described previously (Bird & Ryder 1993). These sections were examined and photographed in a Philips EM 400 transmission electron microscope (TEM).

Feeding experiments

Attempts to determine the feeding habits of *A. guidetti* were made using two possible food sources; *Acrobolus fluitans* grown on *Pseudomonas corrugata* on malt extract agar (Bird & Ryder 1993) and *Rhizoctonia solani* grown on a diluted Czapek-Dox + yeast agar (Wareup 1955).

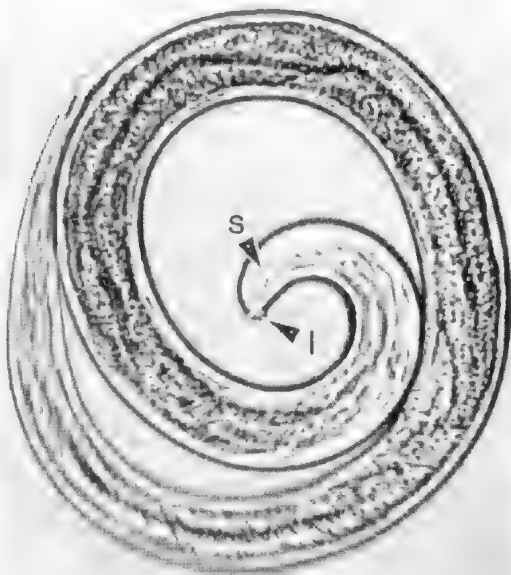
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† Landcare Research, Private Bag 1052, Palmerston North, New Zealand.

1



2



Results

Description

Aprutides guidetti Scognamiglio, 1974
FIGS 1-8

Adult females: Small nematodes, 0.5 mm in length, that exhibit normal coiling and uncoiling in distilled water (Figs 1, 2). When fixed with gentle heat they shrink (about 6% in length and 20% in width) and become slightly curved to C-shaped. Under bright field, photographs of the same living specimen which became coiled after a few seconds (Fig. 2) show the delicate stylet with small thickenings at its base and the lip region bearing a distinct cap characteristic for this species. The latter is seen more clearly in fixed material in glycerol and under interference contrast optics at higher resolution (Fig. 3). This photograph also illustrates the prominent metacarpus with the intestinal junction and the opening of the secretory-excretory pore immediately behind. This opening occurs 57-64 μ m from the anterior end (Table 1). Also clearly visible under interference contrast optics are the vulva and vagina (Fig. 4). Transverse sections cut through the mid-intestinal region and observed with the TEM show that the cuticle is 0.2 μ m thick, becoming 0.5-0.6 μ m thick at the lateral alae (Figs 5, 6). The lateral alae (lateral fields) are distinct, although not pronounced and are 2 μ m wide with three distinct striations, incisures or furrows (lines). The cuticular annulations are fine and spaced about 1 μ m apart. The pharyngeal gland lobe is obscure and extends about 50 μ m posterior to the metacarpus. The intestine is 2.5 μ m in width (Fig. 7) and in the specimens

examined showed little evidence of food material other than a number of multilamellar bodies that occupied the lumen of the intestine (Fig. 8). The lamellae of these structures are approximately 4 nm apart.

The rectum is about 17 μ m in length and so is approximately twice the width of the nematode at the anus. The tail is clavate, tapering and then widening into the characteristic club shape (Fig. 1). It ranges from 39-47 μ m in length and is 4-5 times the width of the nematode at its anus. The vulva protrudes slightly and the vagina is about 7 μ m in length and usually clearly visible at right angles or slightly oblique to the body axis (Fig. 4). The gonad is single and outstretched and consists of ovary with a single row of oocytes, oviduct, spermatheca and uterus all having a total length of 83-103 μ m. The post-uterine sac is collapsed and up to 30 μ m in length. Males were not found.

In an attempt to resolve whether this nematode is a predator or a fungal feeder small numbers were added to cultures of either *Aerobelooides nanus* or the fungus *Rhizoglyphus solani*. However, no growth or development of *A. guidetti* took place in either of these cultures and no feeding was observed.

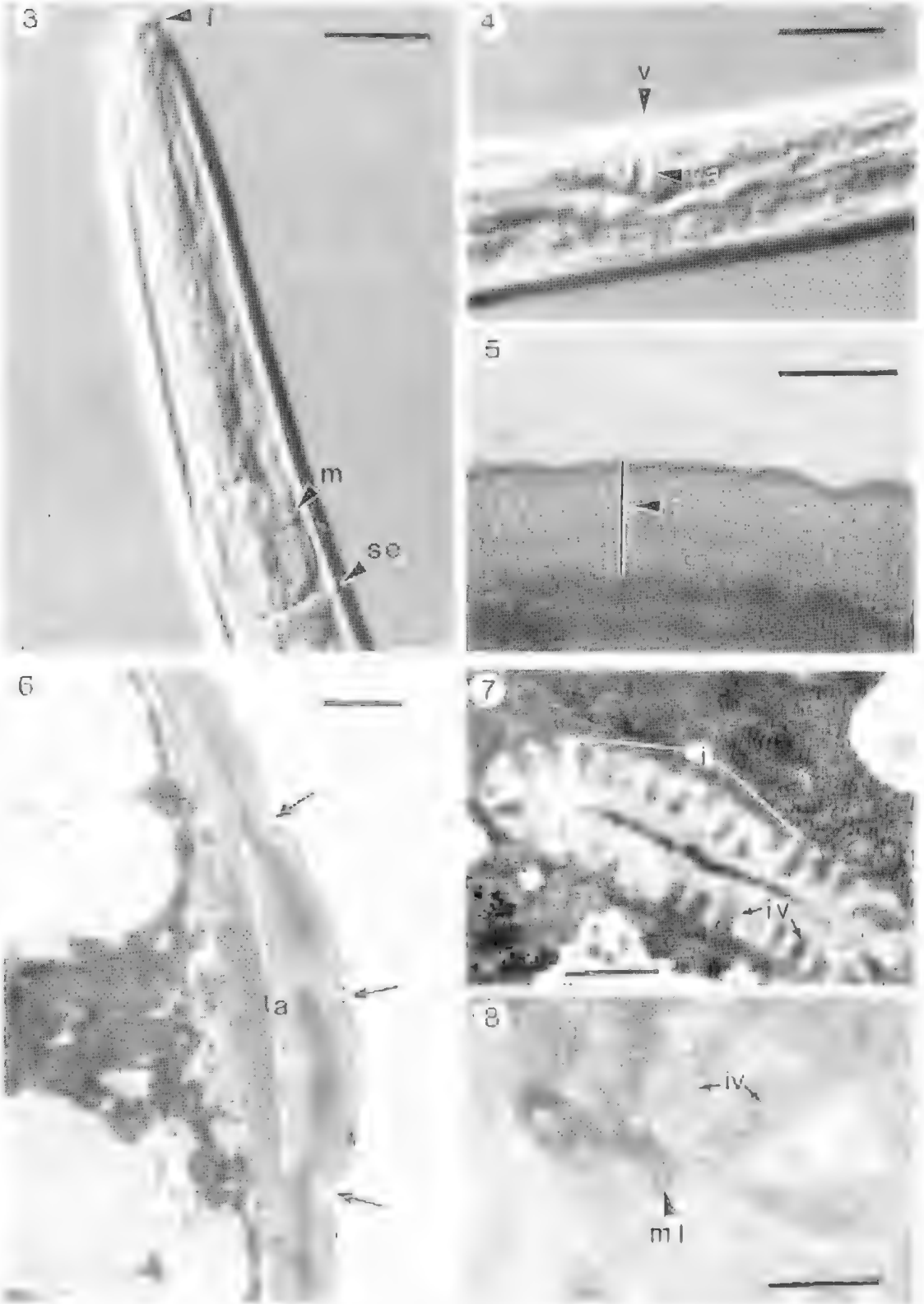
Discussion

There appears to be no doubt that the nematode we have isolated from the heavy clay soil at Northfield is *Aprutides guidetti*. Scognamiglio *et al.* (1970) used the generic name of *Aprutides* after the Latin name *Aprutium* for the Abruzzi region in Italy where this genus was first found. The specific name was after Beniamino Guidetti, a professor of neurosurgery at the University of Rome. Measurements of the nematode found in South Australia are comparable to similar

TABLE 1. Measurements of adult females of *Aprutides guidetti* (μ m).

	n	Range	Mean	\pm SD	(SE)
L	20	395-518	454	34.4	7.7
Maximum body width	20	16-17	16.3	0.5	0.1
Pharynx length	20	54-62	57.6	2.4	0.5
Tail length	20	39-47	43.4	2.9	0.6
Body width at anus	20	9-10	9.3	0.5	0.1
Stylet length	17	12-14	13.3	0.7	0.2
Anterior end to secretory-excretory pore	10	57-64	60.3	2.4	0.7
Anterior end to vulva	20	251-339	299	23.8	5.3
De Man's indices V	20	63-69	66	1.8	0.4
De Man's indices a	20	25-31	28	2.0	0.4
De Man's indices b	20	6.9-9.4	7.9	0.7	0.2
De Man's indices c	20	9.4-11.3	10.5	0.6	0.1
De Man's indices c'	20	3.9-5.2	4.6	0.4	0.1

Figs 1 and 2. Two photographs of a living specimen of adult female of *Aprutides guidetti* taken within a few seconds of each other. Bright field optics showing the anus (a), lips (l), metacarpus (m), stylet (s) and vulva (v). Scale bar = 50 μ m.



measurements made in Italy by Scognamiglio (1974) and in Turkey by Saltukoglu *et al.* (1976) (Table 2). It can be readily recognised under the light microscope by its small size (only 0.5 mm in length), pronounced clavate tail and distinctive cap on the lip region.

The high concentration of this nematode in the heavy clay soil at Northfield (Yeates & Bird 1994), where it made up almost one fifth of the total nematode population, suggests that it is particularly adapted to this type of soil. It is tempting to speculate that *A. guidetti* might have arrived in Australia on the wheels of the Vickers-Vimy bomber that made the first flight from London to Australia as this aircraft landed en route at Pisa, Rome and Taranto in Italy before finally landing at Northfield. This nematode has the capacity to withstand considerable environmental fluctuations in the soil during storage and could have survived in an anhydrobiotic state on the undercarriage of the plane. However, it is unlikely that it was introduced to Northfield in this fashion because the plane landed many times before landing at Northfield. A similar

clavate-tailed nematode has also been detected, albeit in very small numbers (one in 250 counted), in the sandy loam at Avon on land occupied by native shrubs (Yeates & Bird 1994). However, this clavate-tailed form from Avon has not been detected in re-examination of the original fixed material and so no precise measurements to establish its identity have been possible. If it is *A. guidetti*, this would indicate that it is capable of surviving in a range of soils and that it has probably existed in South Australia for some time.

Many species of the family Seinuridae, into which the genus *Aprutides* has been placed, are considered to be predacious (Hunt 1993). This has been observed especially in the genus *Seinura* which has been shown to prey on bacterial feeders such as members of the genus *Acrobeloides* (Hunt 1993). However, the genera *Aprutides*, *Seinura*, *Aphelenchoides* and others are included in the family Aphelenchoididae by Andrassy (1976) and thus this author considers that *Aprutides* and *Aphelenchoides* have characteristics in common. The

TABLE 2. Comparison of measurements of different populations of females of *Aprutides guidetti*.

Parts Measured	Pescara - Italy (Scognamiglio 1974) n = 15		Istanbul - Turkey (Saltukoglu <i>et al.</i> 1976) n = 9		Northfield - South Australia (Present study) n = 20	
	range	mean	range	mean	range	mean
Length (μ m)	379-469	423	330-510	—	395-518	454
Pharynx (μ m)	—	—	47-58	—	54-62	58
Stylet (μ m)	11.9-13.6	13	12.5-13.5	—	12-14	13
Tail (μ m)	32.3-37.1	35	34-42	—	39-47	43
Head to sec-exc. pore (μ m)	—	—	51-64	—	57-64	60
De Man's indices V	66, 1-70.5	68	—	—	63-69	66
De Man's indices a	28-34	30	24-32	—	25-31	28
De Man's indices b	5.4-6.8	6	7.2-9.6	—	6.9-9.4	8
De Man's indices c	11.0-13.5	11.9	9.0-12.2	—	9.4-11.3	10.5
De Man's indices c'	—	—	4.2-4.7	—	3.9-5.2	4.6

Fig. 3. Fixed specimens of female *Aprutides guidetti* in glycerol. Interference contrast optics. Anterior region showing lips (l) bearing a characteristic cap, the prominent metacarpus (m) and the secretory-excretory duct and pore (se). Scale bar = 10 μ m.

Fig. 4. As for Fig. 3 but showing the vagina (va) and vulva (v). Scale bar = 10 μ m.

Fig. 5. Transmission electron micrograph of a section through *Aprutides guidetti*. Showing the cuticle (c). Scale bar = 0.2 μ m.

Fig. 6. As for Fig. 5 but showing a lateral ala (la) and the three distinct incisures (black arrows). Scale bar = 0.5 μ m.

Fig. 7. As for Fig. 5 but showing a section through the intestine (i) and the intestinal villi (iv). Scale bar = 0.5 μ m.

Fig. 8. As for Fig. 5 but showing part of a section through the intestine showing intestinal villi (iv) and multilamellar body (mlt) in the intestinal lumen. Scale bar = 0.2 μ m.

feeding and growth of *Aphelenchoides hyalurgi* on various fungi have been observed and its ability to grow on these different species compared (Bird *et al.* 1989). This would suggest that *Aprutides guidetti* may also be a fungal feeder. In field studies it was assumed that the clavate aphelenchoid, the name given to *A. guidetti* before it was identified (Yeates & Bird 1994), was a fungal feeder. We have not, however, been able to resolve whether this nematode is a predator or a fungal feeder. It is possible that storage of the nematode in soil at low temperature, the misting procedure used to separate the nematodes from the soil and their subsequent handling and duration in water in Petri dishes prior to transfer to the food source, may have inhibited their desire or ability to feed. They appeared active but TEM photographs of transverse sections through the intestine showed that the lumen was mostly occluded and the only contents were a number of multiamellated bodies (Fig. 8). It was not clear if these were the breakdown products of either nematode prey or fungi. Because the digestive and reproductive systems of *A. guidetti* are similar to those of the genus *Aphelenchoides* (Saltukoglu *et al.* 1976) it seems more likely that they are fungal feeders rather than predatory nematodes and the assumption that they feed in a similar fashion to *A. hyalurgi* seems reasonable until evidence to the contrary is forthcoming.

The improved resolution of the TEM has revealed that the lateral alae of this nematode, being 2 µm, are narrower than the previously-reported 2.5–3.5 µm (Saltukoglu *et al.* 1976) and have three distinct incisures rather than two as reported by these workers. In addition, the cuticle is only 0.2 µm thick rather than

0.7 µm although it thickens to 0.5–0.6 µm in the region of the lateral alae. The original measurements of these structures by Saltukoglu *et al.* (1976) were made with the light microscope and are close to the 0.25 µm limit of resolution of this instrument so that precise measurements at these extremes of resolution would have been difficult.

It has been shown that shrinkage in sections of embedded nematodes is about 10% greater than that of unembedded fixed material (Stynes & Bird 1980). However, this discrepancy would only account for a small fraction of the differences that we have recorded in the thickness of the cuticle and lateral alae. Shrinkage similar to that which we have observed due to fixation in females of *A. guidetti* has been recorded in both larvae and males of *Anguina agrostis* (Stynes & Bird 1980) where shrinkage in width was 17% compared to 20% in *A. guidetti*. However, similar heat-fixation and processing through to glycerol of *Anguina agrostis* larvae led to greater shrinkage in length than in *A. guidetti* females (13% compared to 6%). Although it is acknowledged that fixation and processing lead to shrinkage, very few measurements are made on living nematodes because, until recently, it has not been possible to use a suitably fast fine-grain film to obtain them in sharp focus. It is still necessary to use conventional hot fixation, dehydration and mounting in anhydrous glycerol to enable accurate comparisons to be made because this technique has been used to measure the majority of free living and plant parasitic nematodes whose dimensions have been recorded.

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THE HYLID FROG *LITORIA ALBOGUTTATA* (GÜNTHER) IN THE NORTHERN TERRITORY

BRIEF COMMUNICATION

Summary

Knowledge of the diversity and biology of the anuran fauna of the Northern Territory has increased substantially over the past 30 years. In 1961 15 of the currently recognised species had been reported¹ but by 1986 the number had tripled to 45². During taxonomic studies in the late 1960s^{3,4} that contributed to the resolution of the N.T. anuran fauna, a specimen from Alexandria Station identified as *Cyclorana alboguttata* in 1935⁵ was re-examined because it represented the only record of the species in the Northern Territory, and its specific identity has been the subject of dispute⁵⁻⁷. The specimen was demonstrated to be a misidentified topotypic individual of *C. cultripes* Parker, whilst *C. alboguttata* was shown to possess intercalary cartilages, causing it to be referred to *Litoria* Tschudi⁸. The geographic distribution of *L. alboguttata* was plotted from all known museum voucher specimens and demonstrated to be confined to Queensland and northern New South Wales⁸.

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In recent years *L. alboguttata* has been collected on a number of occasions in the Northern Territory at sites near the mouth of the McArthur River in the vicinity of Borroloola, leading to the inclusion of a portion of the western boundary of the N.T. in a revised distribution map⁹. It has also been reported approximately 20 km northeast of Devil's Marbles, considerably further south than the other records¹⁰.

Because the places of lodgement of the specimens on which these locality records are based have not been reported, we provide this information here. The specimens examined are deposited in the Australian Museum, Sydney, (AM), the National Wildlife Collection, CSIRO, Canberra (NWC), the Northern Territory Museum & Art Gallery, Darwin (NTM) and the South Australian Museum, Adelaide (SAM). Methods of measurement follow Tyler¹¹.

All of the specimens of *L. alboguttata* that were examined were taken at two sites. The first is an area of seasonally inundated grassland extending for 10 km flanking the



Fig. 1. *Litoria alboguttata* collected on Carpentaria Highway, 9 km west of Borroloola, N.T. (Photo: M. Davies).

Carpentaria Highway from its termination 1 km south of the Borroloola township, and 2 km east of the causeway crossing of the McArthur River. (Floodwaters flow north into the Rocky Creek catchment, and then east to discharge into the McArthur River - a distance of 8 km). The floodplains extend for only 10 km west, where the Carpentaria Highway rises to pass to the north of the Bukalara Range. From various points along this section 20 specimens have been collected: AM R53214, 53650-52, 53654-62, 54490, 56923; NWC A536, 538; NTM R17749; SAM R33907, 40749. One specimen collected in the Borroloola area by W. J. Freeland (pers. comm.) has been seen by us but its whereabouts is unknown.

The second site is the Mingarda Waterhole on Batten Creek. This waterway arises west of the Carpentaria Highway and the Bukalara Range approximately 50 km from Borroloola. Mingarda Waterhole is near its termination approximately 30 km northeast of Borroloola at the edge of the saline coastal flats. Specimens from that site are AM R53532 and NWC A586-90.

The specimens reported from near the Devil's Marbles¹⁰ (NTM 30446-7) have been examined by one of us (M.J.T.) and reidentified as juvenile *C. australis*.

In the key to frogs of the northeast of the N.T.², *Litoria alboguttata* keys out to *Cyclorana australis*. Both are fossorial species with size ranges that overlap: *L. alboguttata* males 54-67 mm snout to vent length, females 61-83 mm, *C. australis* males 71-79 mm, females 71-102. Each species has an enlarged inner metatarsal tubercle employed for burrowing, but *L. alboguttata* is distinguished externally by its exceptionally rugose skin with short, broad, disrupted plicae on the dorso-lateral surfaces (Fig. 1). In contrast the skin of *C. australis* is smooth apart from narrow continuous dorso-lateral folds. In addition *L. alboguttata* possesses a very narrow vertebral stripe not exhibited by *C. australis*.

We are indebted to the Conservation Commission of the Northern Territory for permits enabling us to collect specimens in the vicinity of Borroloola and to Bill Freeland for advice about his collections there. Out field studies were funded by the Australian Research Council and by Mount Isa Mines Ltd. We thank David Hughes of M.I.M. for logistic support and David Williams (University of Adelaide) for help in the field. For the loan of specimens we thank Ross Sadler (Australian Museum) and John Wombey (CSIRO). The manuscript was typed by Catherine Pascoe.

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